ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

39
1952

binding 4.60

Annals
of the
Missouri Botanical Garden

Volume XXXIX

1952

With 29 Plates, 87 Figures, and 8 Maps

Published quarterly at Galesburg, Illinois, by the Board of Trustees of the Missouri Botanical Garden, St. Louis, Mo.

Entered as second-class matter at the post-office at Galesburg, Illinois, under the Act of March 3, 1879.

MISSOURI BOTANICAL
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Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price	$10.00 per volume
Single Numbers	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

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Volume XXXIX Number 1

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Vol. 39 FEBRUARY, 1952 No. 1

VARIATION AND HYBRIDIZATION IN JUNIPERUS*

MARION TRUFANT HALL**

Introduction

What prompted me to make population studies in *Juniperus?* As a Ranger in the National Park Service, prior to World War II, I was stationed in Platt National Park, Oklahoma, the home of a hybrid swarm between *Juniperus Ashei* Buchholz (called *Juniperus mexicana* Spreng., in 'Gray's Manual of Botany,' 8th ed. 1950) and *J. virginiana* L. Quite naturally, the junipers of the Park proved difficult to classify, and when I began graduate work after the war I found that botanists disagreed as to the identification of junipers in central Oklahoma. The study was begun because of the recognition of so many variants and intermediates between *Juniperus Ashei* and *J. virginiana,* but I had no idea of the extent of the problem until I drove to St. Louis in 1947. Along the way the same variations which I had known in Oklahoma and Texas were seen, again and again, on the knobs, glades, and cliff edges of the Ozarks. I wanted to find out just how extensive was the influence of the two species upon one another.

For such a study the correlation of several morphologic characters throughout the range of the species was chosen as the simplest and most direct means of showing how the plants were varying. This study is one in natural history, based on living plants and mass collections. Evidence of affinity, or lack of it, is circumstantial, not experimental; thus, theories and conclusions must be presented with considerable caution. I have attempted to explain the data in terms of the simplest hypotheses, keeping in mind their correspondences with similar data for other organisms which have been more intensively studied.

There are certain disadvantages in studying variation and evolution in a genus like *Juniperus.* Genetic data such as rate and direction of gene mutation or linkage patterns of multiple factor characters have not been obtained; the cytological

*An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

**Cranbrook Institute of Science, Bloomfield Hills, Mich.

data are meager since little more than a few chromosome numbers are known; the taxonomy awaits population studies for a suitable clarification; and the morphology is really well known for only two species. It is not a convenient group with which to do experimental work such as transplant studies (although widely distributed horticultural varieties may serve as a rough equivalent of transplant material). Students of evolution know that organisms which are well known in a general way are the best material for the study of the forces responsible for the development of discontinuities; whether they are discontinuities between individuals, populations, or higher categories (subspecies, species, or genera), but there are few such organisms. Enough facts have been documented for birds (Lack, 1947; Mayr, 1944) and insects (Kinsey, 1930, 1936, 1937) to give them significant usefulness in studies of speciation. A few plant species, such as those of the genus *Crepis* (Babcock, 1942, 1947), stand as beacons to what is yet to come from thorough studies of many other plants. We know from the many facts obtained from those organisms already analyzed that evolutionary processes are many and variable.

There are certain advantages in studying *Juniperus*. The genus is pragmatically suited to the multiple-correlate type of analysis for several reasons. For population analyses one needs populations. For many organisms these are either uncommon or difficult to find. Junipers characteristically grow in groups of marked prominence in the landscape. Generally, the plants occur in the open and are easily collected. Any one who has stood on an Ozark ridge in winter and looked across an area of old fields, knobs, glades, and cliff edges will appreciate the ease with which populations of *Juniperus* can be found.

The wide use of *Juniperus* as horticultural material is a great advantage in population studies. Individual trees and bushes, horticulturally superior, have been propagated asexually and have been widely grown in parks and gardens. The nurseries of D. Hill & Son (Kumlein, 1939), in particular, have named and propagated various clones. These include well-known horticultural varieties of *Juniperus virginiana*—"Canaertii", "glauca", "pyramidalis", and "pyramidiformia Hilli"; and of *Juniperus scopulorum*—"Moonlight", "Silver Juniper", "Blue Moon", "North Star", "Silver Glow", and "Hill Weeping Juniper". These serve as a rough but effective substitute for transplant experiments, demonstrating what proportions of plant-to-plant differences are caused by environmental influence and what by inherent qualities. Some of these varieties have been widely distributed in many different environments. Usually, they have been propagated vegetatively by grafting, but some have been grown from seed.

Juniperus virginiana var. *Canaertii* is one of those widespread cultigens which makes possible a study of the morphological effects of varied environments. It is a picturesque variety with long, well-separated branches and irregular masses of compact dark-green foliage, and it bears fruit profusely every second or third year. It is propagated by grafting, usually onto a native Red Cedar root system. Three populations of this clonal variety were studied, one in Oklahoma, one in Missouri, and one in Michigan. These data are discussed under "Study of Variation."

In recent years the shelter-belt plantings, carried out under the supervision of the Soil Conservation Service, have consisted of woody plants which could stand the rigorous climate of the great prairie and high plains. *Juniperus* has figured heavily in this development. Farmers from the western Oklahoma wheat belt have noticed the variation in the junipers used for shelter-belt plantings there and some have inquired about it. Three "species" are generally being used: *Juniperus Ashei*, *J. virginiana* (and hybrids), and *J. scopulorum*. In the future one may see small hybrid swarms scattered about farm buildings and shelter-belts in the Midwest and Southwest. One can easily see the value of these plants, especially of the hybrids, in these situations. In such rigorous climates as the high plains, a little of the germ-plasm of *J. scopulorum* coming in from slightly higher altitude to mix with *J. virginiana* produces a plant well adapted to existence on the Llano Estacado. Also, a little of the *Juniperus Ashei* germ-plasm in *J. virginiana* produces a plant which may stand the rigors of western Oklahoma, Kansas, Nebraska, and similar areas where other trees exist on the uplands only with the greatest difficulty.

The general method of studying variation in *Juniperus* is based on Anderson's (1949) "corollary of the demonstration of multiple factor linkage." When germ-plasms are mixed, linkages are a strong barrier to the recombinations of multiple-factor characters. Since the multiple-factor characters generally tend to stay together, the variation patterns in a mixed population tend to fall into three categories: those resembling the one parent, those more or less intermediate, and those resembling the other parent. There may be considerable recombinations and resultant variation, but the degree of both must depend first on the extent to which linkages can be broken.

The term "introgression" was applied by Anderson and Hubricht (1938) to the gradual transfer of genes from one species to another as a result of hybridization (involving repeated back-crossing) at the juncture of the distributions of the hybridizing elements. If introgression is occurring in *Juniperus*, it should be evident in several ways: (1) there should be some kind of evidence that, given the opportunity, the species in question will hybridize; (2) there should be evidence of recombinations of the characters from the two species; (3) the presence of the characters of one species in the other species should be in progressively greater dilutions away from the region of hybrid swarms; and (4), most significantly, the characters which differentiate the two species should be at least slightly correlated throughout the area of introgression.

An analysis of introgression is simplified if the organisms introgressing are very different. *Juniperus Ashei* and *J. virginiana* are easy to analyze since they differ widely in morphology and in ecological preference. As will be shown subsequently, their differences in growth form and in all the classical technical characters used in differentiating species of *Juniperus* are outstanding.

The Species

Juniperus is the third largest genus in the Coniferales and is probably as prominent in the extent of its distribution. It contains approximately forty species though over sixty have been described. The genus has achieved complete northern hemispheric distribution which is a fact undoubtedly related to the value of the berry-cone as a food for birds. It seems to be one of the more youthful genera of the Coniferales since it probably evolved from a transition Cupressoid probably not later than the Cretaceous. Specimens of Upper Cretaceous *Juniperus* have been reported from New England by Hollick (1902) and Berry (1906). Upper Cretaceous fossils of *Juniperus* have been reported from Greenland (Darrah, 1939) which are similar to the modern members of the OXYCEDRUS section. These types were apparently part of the so-called Arctotertiary flora. In America, fossils of the SABINA section of *Juniperus* are known from the Pliocene—the Weiser flora (Dorf, 1938), a transition flora in the Payette formation of southwestern Idaho, contains one species of *Juniperus* apparently the counterpart of modern *J. occidentalis*. From the Pleistocene, specimens of *J. virginiana* have been found in the Don Valley (Berry, 1910; Penhallow, 1907), and specimens of *J. californica* have been reported from the Rancho La Brea tar pits near Los Angeles (Mason, 1927).

The modern xerophytes of the genus have evidently evolved with the development of our modern deserts, apparently during the late Cenozoic, probably since the Miocene. The junipers may have arisen from a transition Cupressoid inhabiting warm temperate regions characterized by winter rains and prolonged summer droughts. The seemingly most primitive species, *J. drupacea* and *J. oxycedrus,* are characteristic plants of what Schimper (1865) has called the sclerophyllous woodlands of the North Temperate Zone. The majority of the species, the appressed scale-leaved ones, are characteristically found in semi-arid regions or in arid regions at mid-altitudes (where microthermal conditions prevail). Exceptions to this climatic generalization are *J. virginiana* and *J. barbadensis,* which occur in subhumid or humid climates and may attain great size, the former tending to occupy the least mesic habitats.

On each continent most of the species are centered about the Pacific side and are nearly equally divided between Eurasia and America. The present distribution of abundance of species in *Juniperus* is best explained by Buchholz' (1948) idea, that the Pacific perimeter probably represents the distribution center of the Coniferales during their most recent speciation cycle.

Endlicher (1847) created three sections in the genus *Juniperus*: CARYOCEDRUS, OXYCEDRUS, and SABINA. These sections constitute an interesting transition series, especially with regard to the female cones and the leaf types. The transitions are from partly woody somewhat cupressoid-like cones in section CARYOCEDRUS to completely fleshy berry-cones in section OXYCEDRUS, and from the acicular-type leaves to reduced scale-type leaves in section SABINA.

The single species in the section CARYOCEDRUS, *Juniperus drupacea,* may represent a relatively unsuccessful attempt at evolution toward a woody-coned form in this predominantly sclerophyllous and xeromorphic genus, or it may represent the sole surviving species of a more ancient group of junipers. This species is confined to the eastern part of the Mediterranean region.

There are approximately ten species in the section OXYCEDRUS, one of which, *Juniperus communis,* is circumboreal. Seven species are found in eastern Asia (China, Japan, Korea), a Pacific perimeter distribution, and two have a Mediterranean coastal distribution but extending through Persia to the Caucasus. The species of this section are characterized by acicular leaves as in CARYOCEDRUS, but they have fleshy berry-cones which are usually close to a centimeter in diameter, intermediate between the twice larger cones of CARYOCEDRUS and the generally small ones of SABINA.

The SABINA section is much the largest, containing approximately thirty species. The majority of these are found in the more mesic habitats within and at the edges of the North American deserts. In the Old World about ten species are found from the Mediterranean to the Himalayas, China, and Japan.

Subdivision of the sections becomes a rather arbitrary matter since the constituent species are all relatively similar morphologically. However, one character is available which clearly separates the species of the SABINA section into two groups. This character is the presence or absence of teeth-like processes on the margins of the leaf—single cells which project out from the other marginal cells at uniform intervals. The more mesic species, *Juniperus barbadensis, J. virginiana, J. scopulorum, J. horizontalis,* and *J. Sabina,* have entire margins while the more xeric ones, *J. californica, P. pachyphloea, J. occidentalis, J. monosperma, J. Pinchoti,* and *J. Ashei,* make a well-marked series from *californica* with very large teeth, to *Ashei* with relatively small ones.

The species discussed in this study include five of those which occur east of the Rocky Mountains. One of these *(Juniperus Ashei)* is a member of the species group with denticulately fringed leaf margins, while the other four *(barbadensis, virginiana, horizontalis,* and *scopulorum)* are generally more mesic and are in the species group with entire leaf margins. Population studies have been made for three of them in regions where each meets *Juniperus virginiana.* Fassett (1944–'45) made studies of populations showing introgression between *J. scopulorum* and *J. virginiana.* The data for *Ashei* and *virginiana* are presented in this paper.

A key to all native species of the SABINA section adjacent to or overlapping the range of *Juniperus Ashei* and *J. virginiana* follows. It was made up from the examination of many specimens, and yet it combines elements of keys from Rehder (1940), Fassett (1945), and Hall (1947).

This key is not constructed for the purpose of differentiating every variant, whether sport or hybrid, but expresses the fundamental differences between the species. For example, *Juniperus virginiana* L. var. *ambigens* Fassett is a trailing to semi-upright shrub generally with the habit of *J. horizontalis* but with the tech-

A. Leaves* with denticulately fringed margins.
- 1. Mature fruit** red or coppery; glands on leaves round, usually ruptured .... 1. *J. Pinchoti*
- 1. Mature fruit blue or blue-black.
  - 2. Leaves glandular; glands elliptic and flat on all leaves; seed light chestnut-brown .... 2. *J. monosperma*
  - 2. Most of the leaves eglandular; glands, when present, round and swollen, especially on the old leaves; seed dark chestnut-brown .... 3. *J. Ashei*

A. Leaves with entire margins.
- 3. Leaves overlapping, tips acute; glands oval or rarely elliptic and shorter than the distance from the gland to the leaf tip.
  - 4. Creeping shrub; fruit bluish, 6.5–8 mm. in diameter .... 4. *J. horizontalis*
  - 4. Upright tree; fruit blue-black, less than 6.5 mm. in diameter.
    - 5. Leaves less than 2 mm. long; fruit 3–4 mm. in diameter, wider than long .... 5. *J. barbadensis*
    - 5. Leaves 3–4 mm. long; fruit 3.5–6 mm. in diameter, very slightly longer than wide .... 6. *J. virginiana*
- 3. Leaves not overlapping, tips obtuse; glands elliptic or rarely oval and longer than the distance from the gland to the leaf tip .... 7. *J. scopulorum*

*Leaves in the key refer only to the mature scale leaves.

**Fruit measurements refer to mature material during its current season, and are made across the fruit, not lengthwise.

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nical characters of *virginiana.* Such names as *Juniperus virginiana prostrata, J. Sabina procumbens, J. virginiana* var. *reptans, J. virginiana horizontalis, J. virginiana* var. *Kasteni,* and *J. virginiana Kosteri,* which appear in horticultural literature or on herbarium specimens originating from the coast of Maine, are to be referred to *Juniperus virginiana* L. var. *ambigens* Fassett (supposedly a variety of hybrid origin). The same situation holds for *Juniperus scopulorum* var. *patens* Fassett, which is a procumbent plant with the habit of *J. horizontalis* and with most of the technical characters of *J. scopulorum.* Fassett considers it as a probable hybrid between the two species.

The taxonomy of the genus is in great confusion for several reasons. First, some of the early botanists made specimens of juvenile or mixed foliage and later described these as new species when actually they represent growth-stage differences within one species. Some of the specimens to which Linnaeus (1753) gave new names were juvenile or mixed-foliaged material. Second, poorly selected material by the collectors usually led to descriptions and illustrations which, particularly before the time of Engelmann, were not adequate to differentiate newly described species from species previously established. Engelmann's (1877) short paper on the American SABINA section is the classic in the taxonomy of the genus. He apparently understood junipers better than any of his contemporaries. Third, once an error became established (published), it tended to be perpetuated. Thus, errors in supposed distribution caused errors in the reference of collected material to species where actual study of comparative morphology was not carried out. Fourth, mistakes are easy to make with junipers, partly because the measurable characters are relatively so small. The leaves are small; the glands are small (near the limit of unaided visibility); the leaf margin differences are almost microscopic; the sporophylls and other structures of the staminate cone and young ovulate cone are likewise minute. There are several large areas of intergradation

between species of *Juniperus* in the United States alone, presumably the result of hybridization. It is well known that extensive hybridization may make a group of organisms difficult to classify. In long-lived plants with efficient dispersal mechanisms, even a small amount of hybridization may be sufficient to make a group somewhat chaotic in its morphologic character patterns. Such plants may give rise to partially hybrid progeny year after year; and many of these progeny may find a hold in nature, especially if they are organisms which are adapted to disturbed environments.

Distribution of the Two Species

The distribution limits of *Juniperus Ashei* and *J. virginiana* are shown in Map I. The method of mapping does not convey a concept of density of distribution, and the density is anything but uniform. Several factors are responsible for variations in the number and spacing of individuals in stands, some of which are discussed under "Population Structure." Both species are probably more abundant now than in the last century because of the cessation of fires and the greater area of

Map 1. Showing distribution of *Juniperus Ashei* and *J. virginiana.*

bare ground as a consequence of the misuse of land. At the same time, there are fewer large plants, since both species have numerous economic properties. The larger specimens of Red Cedar in the South have practically disappeared.

Juniperus Ashei has a disjunct distribution. It forms dense "brakes" which literally cover the Edwards Plateau in Texas, mostly the area represented by the Comanche Series of the Cretaceous, from the Pecos River to Howard County to Palo Pinto County and south along the base of the Balcones Escarpment. Outlying specimens have been reported from Brewster and Terrell counties in southwest Texas, in Garza County along Double Mountain Fork, in Baylor County along the Wichita River, and in Wise County. A gap of nearly 100 miles occurs between populations from the northernmost distribution in Texas and the Arbuckle Mountains in Murray County, Oklahoma. In the Arbuckles it is found on nondolomitic limestones which form fairly deep, well-drained soils with relatively high water-holding capacity. The only other stands occurring in Oklahoma are found nearly 200 miles northeast of the Arbuckles along the bluffs of Pryor Creek near Grand River. The northernmost outposts of Ashe Juniper are the bluffs and bald knobs of the White River in northern Arkansas and in southern Missouri as far east as McVey Knob in Ozark County. The easternmost known naturally occurring *Juniperus Ashei* is on the bluffs of the South Fork Spring River in Randolph County, Arkansas. There are four specimens planted at the Missouri Botanical Garden Arboretum, Gray Summit. Three are from southwestern Missouri, and one from the Arbuckle Mountains, Oklahoma. Whether this species grows in Mexico is not definitely known. It is possible that it might be found across the Rio Grande from Val Verde County. However, Martinez (1946) expressed doubts as to its presence south of the Rio Grande.

In the western portion of its range, *Juniperus Ashei* hybridizes (as judged from morphological criteria) with *J. monosperma* and *J. Pinchoti.* Hybrids between *J. Ashei* and *J. monosperma* have been collected in Texas near Marathon, Brewster County, and at numerous places in Terrell County. Hybrids between *Ashei* and *Pinchoti* have been collected near Comstock, Val Verde County, in northern Kimble County, and along the North Concho River in Tom Green County. A line drawn from Del Rio, Val Verde County, northeast to Fort Worth, Tarrant County, would nearly separate *J. Ashei* from its hybrids with *J. Pinchoti* westward.

Juniperus virginiana ranges from southern Maine to southern Ontario to northern South Dakota to Texas and eastward to the Atlantic Coast. It is a complex species with many variations which show only loose trends. When the variants produced as a result of hybridization are included in the complex it becomes a most heterogeneous species. When Engelmann (1877) wrote that its range was exceptionally great, he was including *J. scopulorum* as identical with *J. virginiana.* However, he also remarked that no other conifer extends through so many degrees of latitude. If the West Indian Lax Juniper *(J. barbadensis, J. lucayana, J. silicicola)* is included as a variety of *J. virginiana,* as some authors have insisted, then Engel-

mann's latter remark takes on added significance. However, typical specimens of *J. virginiana* and *J. barbadensis* Sarg. are quite as different as many other species in the genus, even though introgression has apparently tended to submerge these differences to the casual observer.

Ecology

The ecological story portrayed by the two species is most interesting. *Juniperus Ashei* has rather definite requirements for growth and reproduction, but *J. virginiana* will survive under a very wide range of conditions. The distributions of these species clearly point out the possibility for differences in tolerance to environment. Since all members of the SABINA section require the same basic conditions, in somewhat varying degrees, for establishment (some bare ground or at least thin cover, good drainage, and a high pH), it seems reasonable to assume that, where chances are equal, the absence of one species may be by reason of inherent physiological factors.

The following table furnishes a crude illustration of the relations between the presence of *Juniperus Ashei* and soil type (in all cases calcareous), precipitation, and temperature.

	Av. Ann. Temp. (40 yr.)	Av. Ann. Precip. (40 yr.)	Substrata
Ozark Mts.	56° F.	45 inches	Dolomite (thin soil) knobs and glades
Mayes Co. Okla.	60° F.	40 inches	Non-dolomitic limestone cliffs (no subsoil, rapid drainage)
Arbuckle Mts.	63° F.	36 inches	Non-dolomitic limestone knobs (occur here only on relatively horizontal strata)
Edwards Plateau	65° F.	20–30 inches	Non-dolomitic limestone, massive, porous, cavernous, (on horizontal strata)

As the precipitation effectiveness decreases from the Ozarks to central Texas, the soil factors improve somewhat. The plants will grow on very thin soil (4–6 inches to bed-rock on glades) or on very rocky sparsely covered knobs where the soil type is classified as rough, stony land.

Juniperus Ashei, while quite restricted in its range, produces great quantities of large, palatable berries which are consumed by birds and small mammals. This species has a slight advantage over *J. virginiana* in the production of fruit. In the bald knobs of southwestern Missouri the two species occur together, with their hybrids in relatively equal numbers; but the regions surrounding the knobs are covered with the introgressants toward *J. virginiana* in all age stages, while the most xeric portions of the knobs, the southwest slopes, or a cliff in the vicinity,

are covered with specimens which show the recombinations of characters closest to *J. Ashei.* In the Missouri knob country, the most *Ashei*-like plants always grow on shallow soils containing a high proportion of magnesium carbonates (a dolomite-derived soil). This is the most xeric environment of the region, and this is shown in the structure of the rest of the flora. The knobs and glades support a thin prairie-type flora with many species characteristic of the Southwest. *Andropogon scoparius* and *Bouteloua curtipendula* are common, with some of the bare spaces more or less covered by *Sporobolus ozarkanus.* From this basic cover spring such southwestern plants as *Palafoxia callosa, Centaurium texense, Yucca glauca* var. *mollis, Baptisia minor, Astragalus mexicanus* var. *trichocalyx, Cotinus obovatus, Juniperus Ashei, Petalostemum pulcherrimum,* and *Rudbeckia missouriensis,* along with the more widely distributed plants of barrens and prairie-openings such as *Agave virginica, Isoetes Butleri, Ophioglossum Engelmanni, Psoralea esculenta, Lobelia spicata* var. *leptostachys, Echinacea pallida, Coreopsis grandiflora,* and others. The most common woody plants, other than juniper, are *Ulmus alata, Bumelia lanuginosa, Cercis canadensis, Rhus aromatica,* and *Fraxinus quadrangulata.* Detailed studies of Ozark glades have been made by Brenner (1942) and Erickson, Brenner and Wraight (1942).

The prairie-openings of the Ozarks are like little pieces of the Southwest transferred intact into the Ozark forest region. Floristically and edaphically these knobs and glades are southwestern, yet these open spots are scattered and disjunct. Whole floras cannot migrate inadvertently, but the evidence is overwhelming that the Ozark region extending southwestward into Oklahoma was once much more open and that the ridges and steep upland slopes were eastward extensions of the prairie flora. The facts concerning the migration of whole floras during and following glaciation are being knit together. Pollen analysis is the master key to the late Pleistocene structure of vegetation in glacial and in periglacial regions. Changes in the landscape which have occurred in the last hundred years or so may be inferred from county records and surveyor's notes, from travel notes (e.g. Josiah Gregg's letters, ed. Fulton, 1941, 1944), from Army-sponsored explorations and surveys (e.g. Marcy, 1866; and House of Rep. Ex. Doc., reports on explorations and surveys), from Geological Survey reports, and from many other source works. Suffice it to say that changes in vegetation structure are not only characteristic of past ages but are going on today. A good review of these vegetational changes has been given by Beilmann and Brenner (1951).

In the Arbuckle Mountains of south-central Oklahoma, *Juniperus Ashei* is much more abundant than *J. virginiana.* However, this hilly island of *J. Ashei* is practically surrounded by rather dense local populations of *J. virginiana.* Directly west of the Arbuckles, Red Cedar is not abundant until, beyond the belt of Post-Oak, Black-Jack savannah, it is found on the ridges and hills of the western Oklahoma prairies. The most extensive and dense populations of *J. virginiana* in Oklahoma are found, as in Missouri and Texas, in prairie environments in early stages of succession, in disturbed prairie areas, or in prairie-openings in the savannah and oak-hickory forest.

The Arbuckle Mountain region is classified (for convenience) by Bruner (1931) as Post-Oak, Black-Jack savannah in a prairie climate, even though the vegetation units constitute a complex series of edaphic variants. In regions of critical climate, where climax formations are in transition, external factors such as lithological character, topography, and soil moisture may strongly affect the distribution of the transition vegetation to produce marked zonations (see Warner, 1926). The limestone areas of the Arbuckles show floristic affinities with the Ozark knobs and glades and the Edwards Plateau, even though they are disjunct from both. The Arbuckles constitute a plateau of about 860 square miles rising a few hundred feet above the surrounding prairie with a west-to-east slope from 1,350 feet to 750 feet. This plateau shows a definite mountainous structure with much faulting and folding which have resulted in 12,000 feet of upturned strata giving an unbroken horizontal sequence of sedimentary deposits from Cambrian to Pennsylvanian time. The original mountains were uplifted in the Carboniferous, while the present aspect is the result of erosion which sliced off the synclinal and anticlinal features down to the mountain heart—leaving the differently eroded upturned strata. Cretaceous deposits from epicontinental seas were stripped from the region after late Cretaceous uplift, a consequence of the Laramide Revolution.

The Arbuckle Mountains, with hard-rock truncated anticlines and domes alternating with softer rock synclines and basins, is an outdoor laboratory wherein the effect of lithological factors on the structure of vegetation may be conveniently studied. Each stratum has its own characteristic soil or rough stony covering. Water relations in this region of low rainfall are consequently critical and varied. The line of demarcation between a grassland community on Arbuckle limestone and an oak-savannah community on Reagan sandstone is as fine as a knife-edge. The southwestern species listed above for the knobs and glades of the Ozarks likewise occur on these dry Oklahoma hills. The flora of the Arbuckles shares with that of the Edwards Plateau such plant species as *Juniperus Ashei, Carya Buckleyi, Quercus texana, Rhus copallina* var. *lanceolata, Cercis canadensis* var. *texensis, Abutilon incanum, Psoralea Reverchoni, Dalea frutescens, Lindheimera texana, Forestiera pubescens, Sophora affinis, Fraxinus texensis,* and *Juglans major.*

The occurrence of *Juniperus Ashei* alone in the Arbuckle area deserves an ecological analysis. The species is apparently restricted to two horizons—the Pontotoc conglomerate and the Viola limestone. With the exception of the dolomitic Arbuckle limestone where *Juniperus Ashei* does not occur, these two horizons are the most xeric in the area.

The term Edwards Plateau is used in the most popular sense to include the Comanche Plateau and the Edwards Plateau proper and is roughly the area from the Brazos River south and east to the limit of the Balcones Escarpment and west to the valley of the Pecos River (roughly the Comanchian biotic province, Dice, 1943). The massive Edwards limestone, which is responsible for a magnificent stratum plain in the southern half of the area, is porous, well-drained, and covered with a thin, rocky, chocolate-brown soil of a relatively low organic content.

The distribution of *Juniperus Ashei* a hundred years ago was not the same as it is today (Bray, 1906). In the last century, the Edwards Plateau supported a tall-grass prairie flora and woody vegetation consisting of such species as *Juniperus Ashei, Quercus virginiana, Q. Laceyi,* and *Q. texana* growing on the drier slopes of the much-dissected Balcones Escarpment, and the more mesophytic species in the valley bottoms, canyon floors, and along the flood-plains. As a result of the gradual cessation, or at least control, of fire and because of the thinning of the grass cover through overgrazing, the upland woody species have become established on the Edwards Plateau and in some areas form very dense thickets. Thus, *Juniperus Ashei* now occupies about 4,000,000 acres, probably four times its last-century areal distribution, and some stands are so dense that defoliation of the lower branches results. In the areas upon the plateau where *J. Ashei* has spread, it is associated with *Stillingia texana* except in the "brakes" where there is practically no understory. Competition for water is extremely great in these brakes. When precipitation is long in duration and gentle or when short in duration but rapid, the water does not percolate through the root systems of the junipers. Core drills show that most of this water is absorbed and transpired by the junipers. Both Ashe Juniper and Red Cedar have strong tap roots, but the former has very extensive lateral roots mostly in the surface foot of soil. A "brake" of *Juniperus Ashei* might be compared to a sod-forming grass, and, like the sod, it is relatively well closed to invasion. The increase in range of *Juniperus Ashei* is an important economic problem for the state of Texas, and the ranchmen of the Edwards Plateau are "bulldozing" junipers in order to get a return growth of grass.

The widely varying habitats of *Juniperus virginiana* throughout its range are an important factor in its hybridization. In the Interior Low Plateaus[1] where it is most homogeneous morphologically it is also relatively homogeneous in apparent ecological character. The two habitat types which may be recognized are the forest-clearing and old-field type, which may also be found occasionally on flood-plains, and the glade type, which is typified by the Red Cedar growing on the Lebanon limestone in the glades of the Nashville Basin. This glade type is the more xeric adaptation in the eastern type Red Cedar. The morphological variation between the two types is concordant. Both of these forms are predominantly calciphiles.

In the South along the coastal plain, *Juniperus virginiana* tends to grade into the small-fruited lax-foliaged *J. barbadensis,* which is native to the Florida peninsula and cultivated along the Gulf coastal plain. Sargent (1902) described *Juniperus barbadensis* as: "growing usually in inundated river-swamps and forming great thickets in forests of Taxodium, Red Maple, Gordonia, Loblolly Pine, Swamp Oaks, Palmetto, and Liquidambar." Red Cedar, the lax type, on the coastal plain (1-B[2] area of Map 3) also occurs in swamps, low wet woods, and along flood-plains. In the northern areas (1-H area of Map 3) it grows on sandy soils, dunes, and

[1] The province (after Fenneman, 1938) called the Interior Low Plateaus is here referred to.

[2] "1-B" refers to the introgressants of *Juniperus virginiana* and *J. barbadensis* Sarg. Originally I was using the synonym, *J. lucayana,* hence "1-L" on Map 3.

shore lines, along with *Juniperus horizontalis*. Where limestone is present, it forms extensive stands. In the northwest area of its range (1-S area of Map 3), Red Cedar occurs chiefly on the river bluffs and along ridges. In recent years it has migrated into old fields and overgrazed pastures. In the Ozark region and southwestward, it occurs in a variety of habitats from wet flats to the most xeric knobs or cliff edges. It will be seen that, on the whole, habitat preferences are correlated with introgressing characters.

It is well known that elements of the northern coniferous forest have migrated far south, to Texas and Louisiana, in a pluvial period following the advance of the Wisconsin ice sheet. Pollen horizons (Tharp and Potzger, 1947; Potzger, 1946; Potter, 1947; Deevey, 1949, 1951) clearly indicate that the post Pleistocene vegetation in eastern United States has fluctuated, and correlates with trends in climatic change from cool moist (boreal conifers) to cool dry (pine and oak) to warm moist (beech and hemlock) to warm dry (oak-hickory and grasses) to cool moist. These periods have been named by Blytt (1882) as boreal (cool dry), Atlantic (warm moist), sub-boreal (warm dry), sub-Atlantic (cool moist), and the general theory behind these names became known as the "Blytt-Sernander hypothesis." The maximum of the xerothermic period, corresponding to Blytt's sub-boreal period, has been estimated to be 4,000 to 6,000 years ago.

Whatever may have been the effect of Tertiary or interglacial xerothermic periods on the migration of these southwestern species, it seems reasonable to assume that the present distribution of these elements was initiated by migrations since the recession of the Wisconsin ice sheet, and that these previously more widely distributed elements have since contracted in range to the confines of areas edaphically suitable. It is assumed that the southwestern element has thermic requirements which were satisfied by the sub-boreal and possibly the late-glacial periods.

Some recent work (Cain, 1948; Potzger, 1946) points to the probability that fluctuating xerothermy was the characteristic sub-boreal condition. The distribution of forest and prairie throughout that time expanded and contracted in a minor way, probably remaining fairly closely associated and probably not differing markedly from the modern pre-lumbering forest-prairie distribution. At any rate, the sub-boreal pollen diagrams are characterized by the dominance of oak species with a slight rise in *Carya* and *Pinus* and a fall in *Acer* and *Fagus*. The eastward extension of the prairie (the prairie-peninsula) probably occurred at that time. The southwestern element could have gradually become established in edaphic situations where it could compete with the more characteristic prairie species. The presence of *Juniperus Ashei* in the Ozarks is not hard to explain; however, the presence of the accompanying floristic elements cannot satisfactorily be explained as a fortuitous long-distance migration and establishment in competition with the adjacent prairie species. Also, the existence of habitat continuity is impossible to demonstrate either for recent times or for a xerothermic period.

The most plausible hypothesis, for which there is only a shred of evidence, to explain the presence of the southwestern element on Ozark knobs and glades is

that the migration and establishment occurred when the region was successionally primitive in the late-glacial period. Since the ice-lobes in the middle-western region stopped at so low a latitude, it is not wholly necessary to assume that the peri-glacial area was thoroughly cold, and it was certainly dry. Off-glacier winds mixing with the prevailing southwesterlies would repel and turn the southeast trades and push the storm track southeastward toward the Appalachians and the coastal plain. The peri-glacial area west of the Mississippi may have become colonized by southwestern and more typical tall-grass prairie species at about equal rates. Later, as the Wisconsin ice sheet receded, these southwestern and prairie communities migrated northward along the southern face, the coastal-plain element along the southeast face, and later Red Spruce migrated from the Appalachians north and westward (Cain, 1948). During the boreal and Atlantic periods, these southwestern and prairie floras may have been dissected and reduced by the great increase of the forests (the spruce-fir, pine, and later the oak-hickory). With the advent of the sub-boreal period, the restricted prairie floras may have expanded again, only again to contract to the present distribution.

Evidence of late-glacial tundra (Gramineae and *Artemisia*) has been found by Deevey (1951) in Aroostook County, Maine. This does not mean that a late-glacial flora was characteristic all along the ice border, but the discovery of such horizons, even if they exist, are subject to chance. Also, lacustrine pollen studies have not been made in critical regions such as Arkansas, Missouri, and Oklahoma. This new discovery for North America corresponds to similar evidence gathered by Degerboel and Iversen (1945) on the presence of late-glacial (Late Dryas) dry-steppe vegetation (Gramineae, *Centaurea Cyanus, Helianthemum oelandicum, Artemisia campestris,* and *Hippophae*) in Denmark. With the refinement of pollen analysis in America (surer identification, surer separation of pollen curves, more sensitive intervals), the late-glacial period may become more clearly defined.

The northeastward migration of the southwestern element was related to the presence and continuity of suitable habitats which were probably not only more wide-spread than today, but were also continuous. The most rapid migration of the xerophytes occurred along the uplands, and those plants such as juniper, with efficient means for dispersal, were the pioneers. Subsequently, as climatic conditions became more mesic, the woodland encroached, but frequent fires were very effective in slowing or preventing this encroachment. In modern times, as fires have become less a factor, the woodland has blanketed even the uplands, with the exception of the glades and knobs which are edaphic barriers to forest succession, leaving old open-growth Chestnut Oaks well hidden within the dense forests. Yet, fundamentally, the southwestern element of the flora is distinct and separate from the eastern and southeastern as pointed out by Adams, 1905. The most significant consequence of the northeastern migration of southwestern elements was the bringing together of species which had apparently been isolated from one another for a long time. The results might well have been a "freshening" of the germ-plasm of those species.

Population Structure

Populations of junipers were sampled wherever the individuals were so numerous that random mass collecting was possible. In almost every population collected, the individuals were closely spaced in the cedar-woodland or cedar-brake type of stand. Isolated individuals were examined but not scored. Scattered individuals in oak-hickory woodland were studied but not scored as population pictograms. The distance between individuals in a population varies from widely spaced to so close that the branches touch all around. The amount of bare ground or thin cover determines their potential density in a stand.

Generally, junipers are found in areas which are in some early stage of succession or where a marked disturbance of the environment has occurred. The structure or pattern of any particular population depends on a number of factors, some inherent and others circumstantial. Junipers are classed as shade-intolerant plants. They grow best on well-drained, neutral, or alkaline soils. They have both deep roots and surface roots which enable them to compete successfully with bunch-grasses but not with sod-grasses. Therefore, these plants make the best growth as individuals and make the densest populations in dry, rocky soils with sparse cover or with clumps of vegetation surrounded by bare ground. Certain circumstantial factors affect the pattern of the population. Birds, especially the Thrush group, are the principal agents of dispersal of juniper seeds, but mammals, water, and gravity may play an important part. Populations spread, where topography allows, through the establishment of seedlings from seeds deposited by surface run-off water. The role of mammals, rabbits in particular, as disseminators of juniper seeds has been considerably underestimated. Wolf (1947) has made detailed studies of dispersal in two species and found that in open treeless country, rabbits are more important dispersal agents than birds.

If one assumes that in pre-human times fires were infrequent and the landscape was generally less disturbed than in modern times, the juniper was very likely confined, because of the pressure of competition, to the natural bad-lands such as cliff-edges and steep, rocky slopes. With the repeated burning-off of land in recent time, only those junipers remained which were in locations inaccessible to fire. In the last fifty years, fires have been substantially reduced and new areas have become available for invasion by the juniper. The source plants for recent migrations were those occupying cliff-edges and cliff-walls or in protected places. The present distribution of the most ancient specimens seems to bear this out.

COMPARATIVE MORPHOLOGY OF *Juniperus Ashei* AND *J. virginiana*

The differences between *Juniperus Ashei* and *Juniperus virginiana* are so great that one is almost unprepared for the fact that the two species hybridize so readily. The following table outlines some of the more outstanding differences.

Juniperus Ashei	*Juniperus virginiana*
1. Trunk more or less branched near the base; aspect generally bush-like; height to 35 ft.	1. Trunk single, erect; aspect generally pyramidal; height to 80 ft.
2. Foliage dense.	2. Foliage more or less open or plume-like.
3. Foliage yellow-green.	3. Foliage bluish-green.
4. Glands on leaves uniformly round, raised well above the leaf in a hemisphere.	4. Glands much elongated on certain leaf types, elliptic on others, seldom raised above the leaf.
5. Fruit large (6–8 mm. in diam.), with slightly resinous juicy pulp.	5. Fruit small (3.5–5 mm. in diam.), with strongly resinous dry pulp.
6. Seed 4–5 mm. in diam.; 1, rarely 2, per berry-cone, sharply pointed tip, no pits, smooth white hilum conspicuous, covering the seed at least one-third its length from the base.	6. Seed 2–3 mm. in diam.; 1 or 2 per berry-cone, rarely 3–6, blunt tip, numerous pits, small inconspicuous hilum.

Several of these differences merit further discussion.

1. BRANCHING PATTERN:

In general, investigators have considered a plant as either branching or unbranching and have let it go at that. When studied carefully, however, the branching pattern in *Juniperus* proves to be a character of value in separating not only species from species but also inter-specific hybrids from the parent species. In this study the central stem will be referred to as the primary shoot (axis); the main branches from the axis, whether in excurrent branching forms or multistemmed forms, will be called the secondary shoots (second degree of branching); the lateral branches from the secondary shoots will be called the tertiary shoots (third degree of branching) (fig. 1). The branching pattern in most junipers, especially of the SABINA section, is terminated by branching of the seventh degree (fig. 2). The more mesic species, *Juniperus virginiana,* may have branching to the fifth or sixth degree (fig. 2).

In *Juniperus* the vegetative portions of the plant are differentiated into short shoots ("spurs") and long shoots ("whips"). This difference is not as noticeable as it is in *Ginkgo* or *Pinus,* but the extremes of any one individual are quite as different from each other. In each species of *Juniperus,* leaf shape on the spurs differs from that on the whips. This has not been clearly indicated in most morphological treatments of the genus. In fact, adult whip foliage has been widely confused with juvenile foliage. The terminal portions, the long shoots or "whips", of the secondary shoots which are usually sheathed by a particular kind of elongated leaf, are called "terminal whips." The lateral branches of the secondary shoots, the tertiary shoots, may also be terminated by leaves of this elongated type, and these tertiary-shoot terminals will be referred to as the "lateral whips." Not all secondary shoots have terminal whips; for example, very old ones and those which have lost the terminals by accident or as the result of insect damage (twig borer).

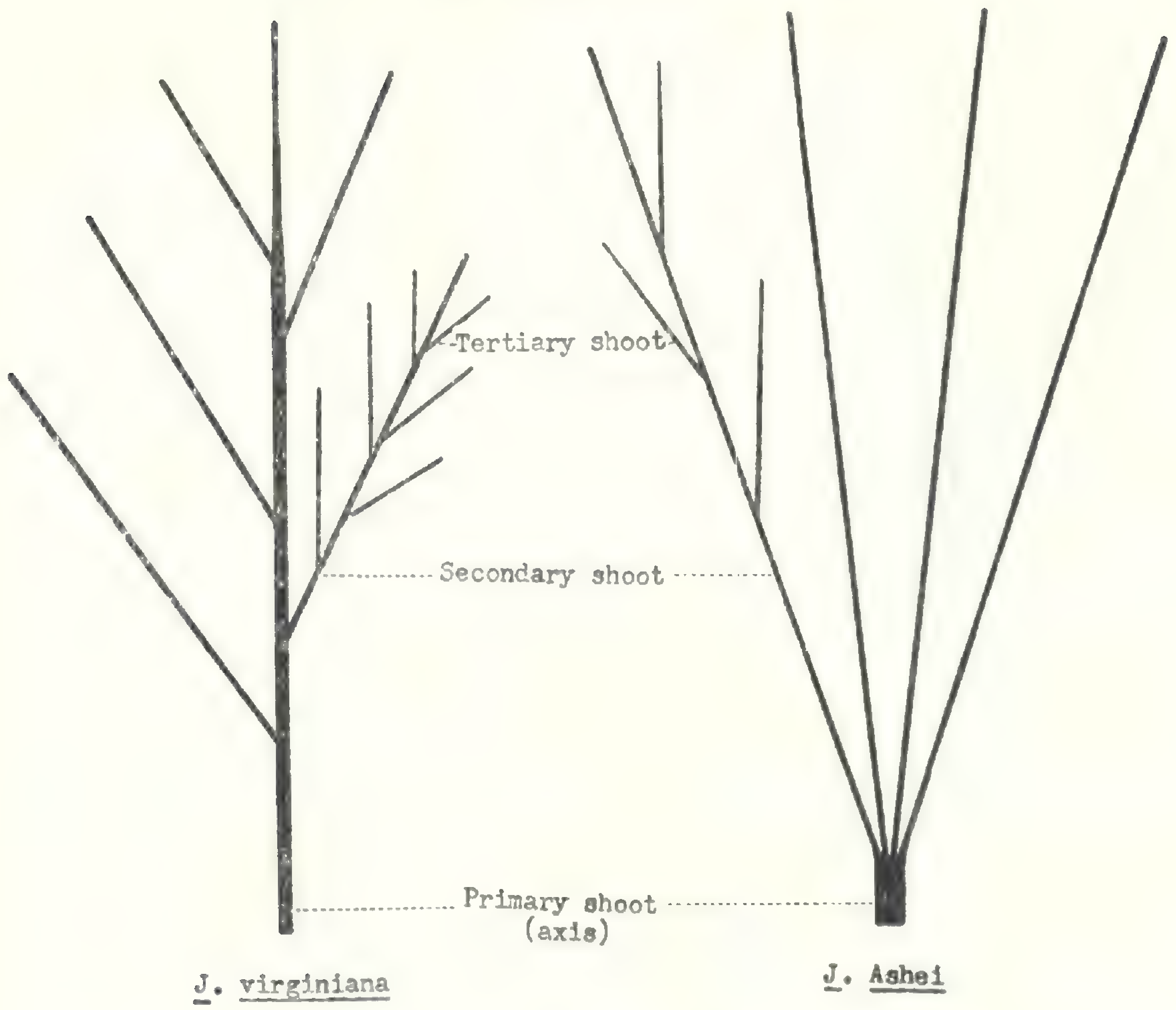

Fig. 1. Diagram of branching pattern.

Degree of branching was studied to determine whether there was any difference in this character between the two species. *Juniperus Ashei* was found to have a slightly greater degree of branching than *J. virginiana* (fig. 2). However, the tertiary shoots and their laterals are generally much shorter in *Juniperus Ashei* than in *J. virginiana*. The short branches of *Juniperus Ashei* give a dense, almost solid appearance and the long branches of *J. virginiana* a plume-like aspect.

Straight-trunked specimens of *Juniperus Ashei* are found only when the individuals are crowded so severely that defoliation of the lower branches results. Also, specimens are sometimes found with branches apparently diverging from a point at the ground level. Plants which in their early seedling stages have been grazed by goats or other animals have a bushy much-branched habit. Wolff (1948) reports that seedlings of *Juniperus Ashei* which have been cropped by goats make a growth resembling that of *J. Pinchoti*, the Redberry Juniper. He states that in such areas the two are so much alike in habit that other characters must be used to distinguish them. Usually, branches come out from a moderately buttressed axis close to but slightly above the ground level. These branches diverge and arc upwards in such a way that the plant looks like a giant tumbleweed. The tertiaries usually leave the secondaries or major branches at a wide angle, often at 90°. They apparently grow outward half their total length or less and then arc upward,

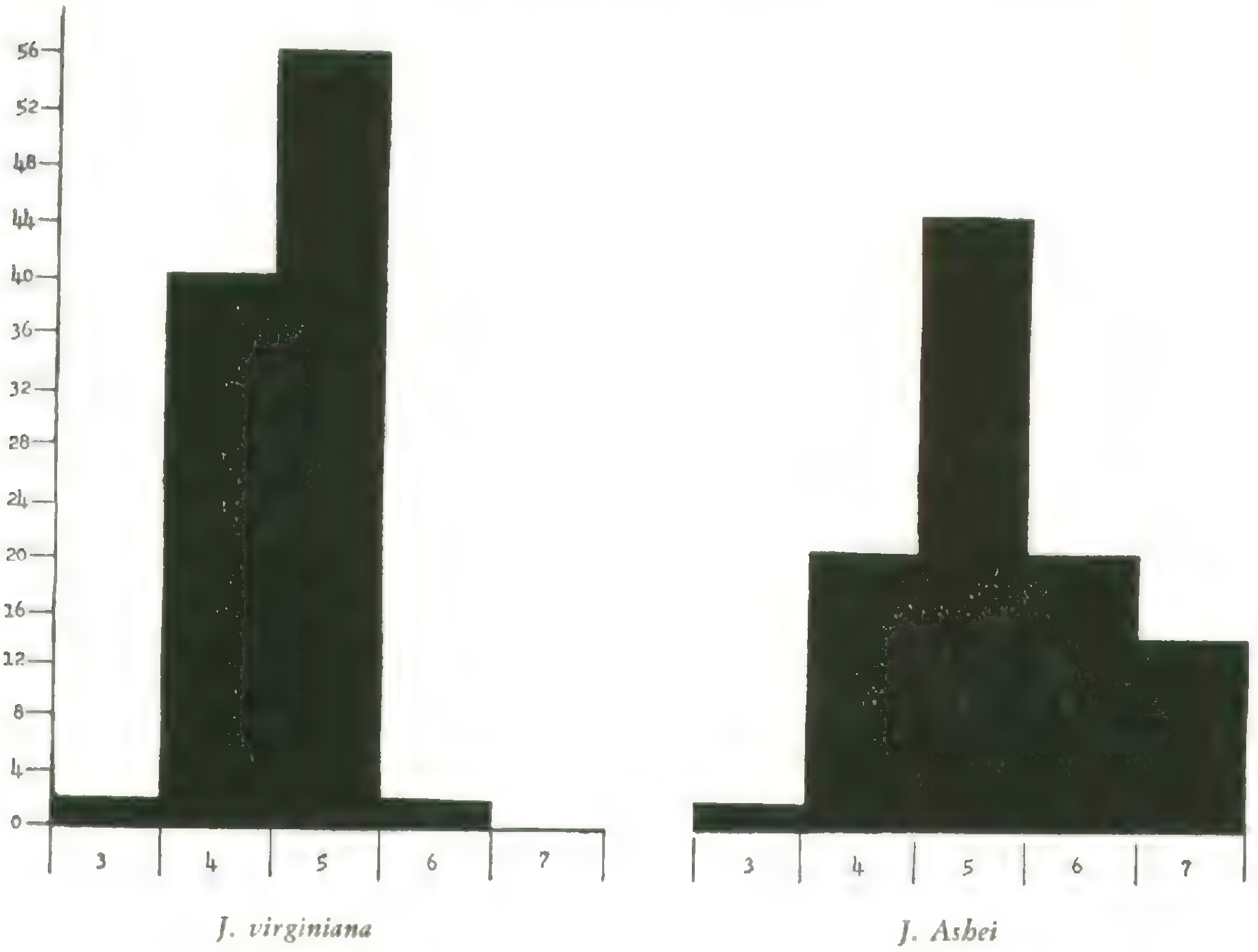

Fig. 2. Degree of branching based on counts from 100 tertiary branches of *J. virginiana* and of 100 branches of *J. Ashei*. Ordinate values represent frequency; abscissae, degree of branching from the major axis or axes.

further contributing to the dense bush-like aspect. The bark is often covered with a white patchwork of rings and splotches caused by a fungus, *Cyanospora albicedrae*. It is least prominent on plants of the bald knobs and White River bluffs of southwestern Missouri, and its occurrence on *Juniperus virginiana* is almost negligible. Some of the most bushy plants with very thick blunt branches but having technical characters more like eastern Red Cedar have been found heavily infected with *Cyanospora*. The most dense splotching occurs on the branches of pure *Juniperus Ashei* of the Edwards Plateau in central Texas. An Ashe Juniper infected with cedar-apple rust has never been reported.

The southwestern species may get to be 35 feet in height. On the Edwards Plateau most of the large old Ashe Junipers have long since been chopped and used for sills, railway ties, or posts. Approximately 4,000,000 acres of the Plateau adjacent to the Balcones Escarpment are now covered with cedars in various stages of maturity. A 4-inch basal trunk with 3½ inches of heartwood may be 50 years old. This corresponds to a 6-inch trunk at 50 years in *Juniperus virginiana* in Virginia. Likewise, if secondary shoots are cut the same distance back from the tip in *Juniperus Ashei* and *J. virginiana*, those of the former will be found to contain at least one and usually two more annual rings than those of the latter. Both species grow fairly rapidly, with eastern Red Cedar taking the lead.

Seedlings of *Juniperus Ashei* two feet tall may have from 7 to 9 well-developed, often eccentric, annual rings. Most of these seedlings have as much adult foliage as juvenile. The condition in Red Cedar is quite different. In Kentucky and Virginia, 2-foot seedlings have 4 or fewer annual rings and only juvenile foliage. On the Tennessee glades of the Nashville Basin ring transitions occur in slightly smaller-sized plants than characteristic of the "forest" tree type. However, on the bluffs and glades in the Ozark region and southwestward, 2-foot seedlings have 6–8 annual rings, and occasionally a specimen is found with slightly eccentric rings. In the same areas, where conditions are favorable, the seedlings develop in the fashion characteristic of the eastern forms. Now these phenomena can be readily explained as habitat responses; even the plants with eccentric rings may be suffering from severe root retardation on the short-radical side, which might correspond with the bluff side. But on the glades, many of which are relatively uniform habitats, these differences exist together. In hybrid swarms they are most obvious.

Juniperus virginiana in its typical form is a forest tree of stately proportions. In mesic habitats, such as the Interior Low Plateaus of Tennessee and Kentucky, it may reach a height of 80 feet or more and basal diameters up to 2½ feet. The aspect of eastern Red Cedar is indeed striking when compared with the shrubby or bush-like habit of most species in the genus. The lower branches on mature specimens growing in the open are quite long and usually arc downward about two-thirds their length and then upward to the tip. The bulk of the photosynthetic surface is then oriented in a plane tangent to the radial circle, which in effect makes the whole branch somewhat bilateral and contributes to the symmetry of the uniformly columnar crown and at the same time produces a maximum of green crown surface.

From the evidence based on clones of horticultural material, habitat does not seem to have a very great direct effect on habit, but in natural populations there are certain growth forms which seem to have been selected for particular habitats. In the Interior Low Plateaus of eastern United States there are two distinct habitat forms. One is the tall columnar tree found in open woods on relatively sandy or rocky limestone soils which do not support dense deciduous forest stands, or else on land which is kept cleared of forest by one means or another employed by man. Then there is the eastern glade or "barrens" form which is much less majestic, rarely being over 40 feet tall with secondary branches coming close to the ground. Of the glade plants, the lower branches are much longer in relation to the height of the tree, giving a more striking pyramidiform aspect. There are also recurrent types within these well-defined biotypes. The weeping form is commonly found in the lowest, wettest habitats, along creeks, rivers, or at the edges of swampy places. Sometimes, it occurs apparently at random in a population where no habitat factors seem to be involved. This weeping form is common to the genus as a whole and examples may be found in many species.

Symmetry of growth is of considerable importance as an aid to the study of introgression. The repeated branching system which is a prominent characteristic of the Cupressaceae and of *Juniperus* in particular is an interesting study by itself. One can determine by looking at the habit of each species what form the secondary and even the tertiary branches will display. In general, the branching system is repeated from the primary axis to the secondaries and the tertiaries. To prove that this is so does not require elaborate measurements. Several colleagues were invited to try grouping these secondary branches from each of five individuals into the five categories representing material from the individual plants. I had selected secondary branches from around the tree at a particular level and labeled them with an inconspicuous coding. After these branches were mixed, the sorting began. In every case these specimens were re-arranged into their original groups. The best method used was simply to hold the specimens in silhouette to the sky and compare their basic branching patterns. In *Juniperus* the exactness with which the replication of branching occurs throughout the plant depends on the relative purity of the species, for in areas where the species were thought to be relatively pure the replication was good, while in areas where hybrid swarms existed it was less exact. I was able to use branching system as a quick reference or clue to the relative degree of variability in a population.

Another method of demonstrating the replication of branching throughout the tree is to make drawings to the same scale of a number of branches of different order or degree and compare them with the same scale-drawing of the whole tree. This is laborious, but it gives measurable evidence of the importance of the branching pattern in variation studies in and between higher plant species. Such drawings were made of plants from near Glasgow and Bowling Green, Ky. (typical *Juniperus virginiana*); Grenada, Miss. (typical *J. virginiana*); Lesterville, Mo., and Gray Summit, Mo. (the Ozark type *J. virginiana*); Eagle Rock and Cedar Valley, Mo. (hybrid swarms); Busch, Ark. (hybrid swarm); Platt National Park, Okla. (hybrid swarm); Arbuckle Mountains, Okla. (typical *J. Ashei*); Kerrville, Tex. (typical *J. Ashei*); and New Braunfels, Tex. (hybrid swarm). The tree-to-tree and intra-individual variations in branching patterns showed the following trends: (1) least in populations of the two species away from the range of distribution common to both; (2) greatest in populations known to be hybrid swarms; (3) intermediate in areas suspected of having the influence of *Juniperus Ashei* even though no native specimens were in those areas. The area to which item (3) above applies is the central and northeastern portions of the Ozark Plateau. The tabulation and grouping of this initial data were preliminary to the population studies set forth in this paper.

With branching pattern data, one may distinguish between *Juniperus Ashei* and *J. virginiana* with 100 per cent accuracy, between individuals within either species with accuracy of about 90 per cent. Because of such symmetry, there are a great many similar branches at various levels on the tree which enables one to sample material reasonably free from environmental variables.

In most good species of higher plants, those with discontinuous differences and with simpler variation patterns than those of a species complex, this relatively accurate replication of branching within individuals may be a fundamental character for contrasting each against the other. It is the presence of disharmonic variation (the lack of accurate replication from branch to branch) which gives the first clue that a particular individual may be a hybrid. Interspecific hybrids in *Juniperus* are more variable within themselves than are pure individuals. This disharmonic variation is probably the result of the conjoining of two different systems of growth. Such ideas have been elaborated upon by D'Arcy Thompson (1942) and Huxley (1932). The less extensive or more subtle the introgression the less obvious is the morphological or physiological expression. This clearly indicates the inter-dependence in science of data from various sources. If it had not been for the years of work in groups of organisms which could be tested with expedience (Heiser, 1949), it would be nearly impossible to understand what has happened in *Juniperus*. Even hybrid swarms among the species are difficult to study, but they offer rich material as to what happens when germ-plasms are mixed up. In *Juniperus* the most obvious situation is in the hybrid swarms of *J. pachyphloea* and *J. scopulorum* in east-central Arizona and west-central New Mexico, where a juniper which resembles live-oak in bark and branching characters, with fruit as large as a pecan, is hybridizing with another juniper which looks quite like eastern Red Cedar. The most obscure picture is that of the hybrid swarms of *Juniperus scopulorum* and *J. virginiana* in the middle-western United States. Here the Red Cedar and Rocky Mountain Juniper are so similar as to require practically a statistical study of their characters to separate them.

2. Foliage Density:

Foliage density is a very good character to delimit the species in the field and even offers aid in spotting recombinations. Although such a character is not free from environmental modification, direct or indirect, when density is contrasted with other characters on the same specimen, some information comes to light which is not to be found in most examples of progressive adaptation to xeric conditions. For occasional individuals in populations known to be hybrid swarms, on McVey Knob, Branson knobs, and Platt National Park, the density may vary on a single plant all the way between that characteristic of each species. This tendency also holds for other characters. The difference in density is primarily due to the number of laterals per unit length of the secondaries or tertiaries, and this is again related to the comparative growth rates of the two species. Thus, in *Juniperus Ashei* there are many more lateral branches per unit length of the secondaries and tertiaries, and these typically are considerably shorter than in *J. virginiana*. When length of laterals is plotted against number of laterals, the values for *J. Ashei* do not overlap those for *J. virginiana* until values for the populations on the Ozark glades are interjected.

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Three selected populations were studied in detail in relation to foliage density, an open field and a glade population of *J. virginiana* at the Missouri Botanical Garden Arboretum at Gray Summit, near St. Louis, Missouri, and a population of *J. Ashei* on the Edwards Plateau near Kerrville, Texas. At the Arboretum the open field and glade population are only two miles apart; yet the foliage density in the open field group is like that in eastern Red Cedar while that of the glade group is clearly intermediate between the eastern and the southwestern species. The habitats are not the same by any means. The main thing they have in common is that each is largely covered by grasses and junipers.

3. Foliage Color:

The color forms in *Juniperus virginiana* are too numerous to treat here. For purposes of contrast a few generalizations will suffice. Typical eastern Red Cedar is dark green, frequently with a slight bluish tint. One common color form found throughout the range of species is the bluish-glaucous one. Yellow tints are rare in *Juniperus virginiana.*

Juniperus Ashei is a deep olive green with a conspicuous yellow cast except in hybrid swarms. In hybrid swarms there are found some plants (taxonomically *J. Ashei*) with blue-glaucous foliage and some with very dark green almost black foliage growing side by side with plants having the typical *Ashei* color form seen in the Arbuckle Mountains or the Edwards Plateau. These color recombinations are especially noteworthy in the bald-knob country of southwestern Missouri (Bald Knob southwest of Hollister on Highway 86).

The color of the portions of those shoots which are just becoming woody is a fairly dependable character for contrasting the two species. Young woody twigs of eastern Red Cedar are typically dark brown, usually tinged with gray but sometimes with red. The young twigs of Ashe Juniper are a bright conspicuous rust-brown. As they age they become gray until finally they have an ash-gray hue.

Because of the highly subjective nature of color judgment, even with the aid of complete color charts frequently used in animal taxonomic work, color characters were not utilized in the pictorial population graphs.

4. Glands:

The glands are good characters for contrasting the two species, both the whip-leaf glands and spur-leaf glands being quite different in their typical form.

Whip-leaf glands.—In Red Cedar these are typically much longer than wide. On vigorous whip shoots the leaves are 10–14 mm. in length. The ratio of gland length to gland width ranges from 6 to 12. In typical *Juniperus Ashei* these leaves are from 4 to 7 mm. in length, rarely 8 mm., while the ratio of gland length to width is usually 1, sometimes 2 (fig. 3). This means that in the eastern species a leaf 12 mm. long may have a relatively flat, elongate-elliptic or tear-drop gland on the back side 6 mm. in length and 0.6 mm. in width, a ratio of 10. Usually, this gland extends toward the tip of the leaf past the juncture of the sheath and

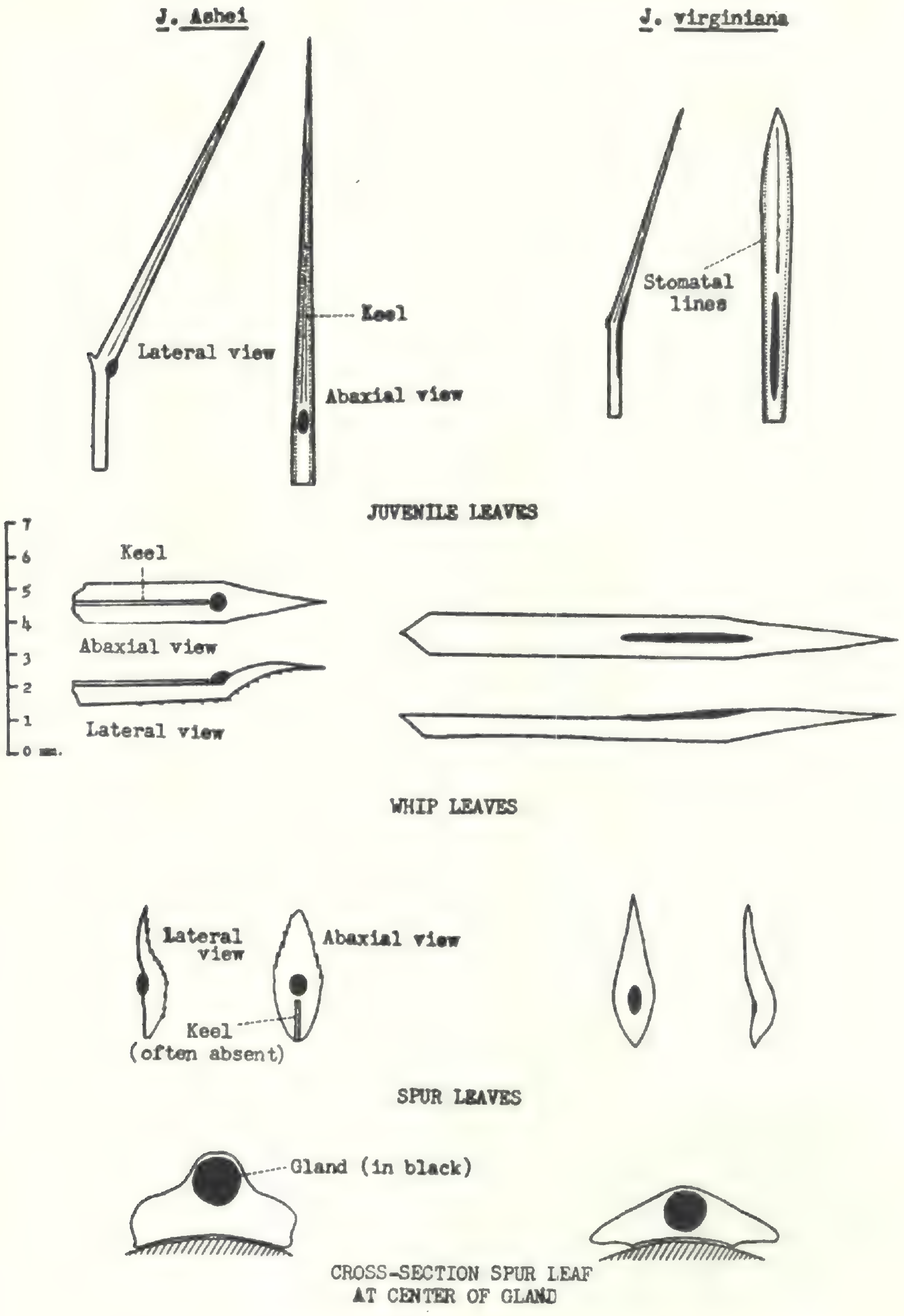

Fig. 3. Leaf morphology of *Juniperus Ashei* and *J. virginiana*.

the blade. In the southwestern species a leaf 7 mm. long may have an almost perfectly round raised gland from 0.5 to 1 mm. in diameter. The gland gives the appearance of a small BB shot placed on the back of the leaf at the juncture of the sheath and the blade.

In hybrid swarms the gland measurements vary between the values for the two species along with many unusual combinations of the other characters. In the areas where influence of *Juniperus Ashei* is suspected in *J. virginiana*, the gland measurements are intermediate.

Spur-leaf glands.—In Red Cedar these are typically elliptic, flush with the lower surface of the leaf, and rarely exceeding 1 mm. in length. They are invariably farther than their own length back from the leaf tip. In Ashe Juniper the spur leaves may be glandular or eglandular. If glandular, the glands are usually slightly less than 0.5 mm. in diameter and are situated at the juncture of the sheath and the blade. They are also slightly raised above the abaxial surface of the leaf but not so much so as on the whip leaves. Well within the range of the species these leaf glands vary but little, but at the commissures of distribution of the two entities many interesting variations occur, sometimes within a single plant. In hybrid swarms, specimens of *Juniperus Ashei* are found without eglandular leaves but with typical glands on some spurs and elliptic raised ones on others. Leaves of *J. virginiana* in such a location are never eglandular, but the glands are even more variable though often very small and inconspicuous. In some of the *virginiana*-like hybrids, glands may be found here and there which, if considered alone, would identify the specimen as *Juniperus Ashei.*

5. Fruit:

Most Junipers are dioecious. However, both megasporangiate and microsporangiate strobili are often found on the same plant, but one or the other type is always in much greater abundance. The seemingly simple fruit of *Juniperus* is such a morphologically complex structure that an analysis of its variation must be preceded by a technical discussion.

In the sabina section the megasporangiate cone is generally formed from six scales. The cone appears in the fall, borne terminally on dwarf or short axillary shoots from branches of the current season. The sporophylls become recognizable only a few weeks before pollination, when at least two pairs of them grow up over the ovules and coalesce to form the berry-cone. The berry-cone consists of two or more pairs of opposing sporophylls. The fertile sporophyll-pairs are central on the cone axis with sterile sporophyll-pairs above and below. Sometimes only one sporophyll of a pair is fertile. When the berry-cone approaches maturity, the "fruit-scales" appear on what is morphologically the upper side of the sporophylls and contribute the bulk of the fleshiness of the mature structure.

The young buds become visible just prior to pollination. As the fruit scale primordia grow, the sporophylls are pushed away from the ovules making them plainly visible in their "nest." Later the "fruit-scales" grow up over the ovules

and seal them within the "berry." In some species the sporophyll tips are quite plainly visible about the sides of the berry-cone, while in others they are almost imperceptible.

The fruit of both *Juniperus Ashei* and *J. virginiana* matures in one season. In both species flowering occurs annually, but the extent of the crop varies a great deal from plant to plant and from year to year. Usually, a heavy crop is produced every third year. The southwestern species bears much larger crops of fruit which frequently appear as dense "clusters", giving the aspect of bunches of grapes.

In *Juniperus Ashei* the young ovulate strobili appear from mid-winter to mid-spring and may be found fully ripened from September to December. There seem to be no critical factors affecting flowering time decisively. Both Ashe Juniper and Red Cedar begin to flower later in Missouri than in Texas. Because of the overlap in flowering time, plants of the two species, wherever they occur together, may utilize pollen of either or both. By mid-February the staminate cones have shed their pollen.

The ovulate cone consists of 3 ternate scales (a single whorl) or, more commonly, 2 pairs of decussate scales. The sporophyll tips or scales (those which become a tiny flap on the fruit coat) are finely toothed on the margin. The lower sporophyll pair usually has one fertile member resulting in a single-seeded berry-cone. Often the two upper bracts or leaves contribute to the fleshy mature "berry," but they invariably remain at the very base of the fruit. Just after pollination the sporophylls elongate rapidly, so that the young cone becomes about twice as long as wide and looks like a tiny urn. Then the fruit scales begin to grow and completely close over the ovules, pushing the sporophyll tips apart and increasing the girth of the fruit. Generally, the length of the mature berry-cone is 1 mm. more than its width, which may be from 6 to 8 mm. The sporophyll tips are very conspicuous in the fresh, mature berry-cones but with age may slough off or dry up.

In *Juniperus virginiana* the young ovulate strobili become evident toward the end of February just prior to pollination, which in the Ozarks generally occurs the first week of March. Ottley (1909) reported that seasonal variation in pollination time in *J. virginiana* amounted to as much as two weeks in Massachusetts. Spatial variation in the occurrence of stages of the reproductive cycle is quite marked. In general, there may be as much as a month's difference in time of flowering, pollination, fertilization, and final ripening, from Texas to New England.

The cone consists of two pairs of sporophylls, one or both of the lower pair being fertile, while the upper two are sterile. Sometimes a third pair develops, resulting in a cone with the fertile pair of sporophylls tipped by 2 pairs of sterile ones. The mature berry-cone often shows 6 tips or wrinkles on its fleshy periphery. This usually reflects the role of a pair of subtending bud scales in the construction of the cone. Ordinarily, there are 4 wrinkles or tips which are the remnants of the sporophyll tips after the growth of the fruit scales.

Mathews (1939) has described three types of flowers for *Juniperus virginiana:* (1) with one ovule in the axil of one member of the fertile sporophyll pair, (2) with two ovules side by side in the axil of one member of the sporophyll pair, (3) with one ovule in the axil of both members of the fertile sporophyll pair. He reported that about two-thirds of the flowers were of type 1, and the rest were divided equally between types 2 and 3. These observations seem to be best supported by the plants in southern and southwestern areas. The flower types were usually distributed in such a way as to be relatively constant for a particular tree. Either the types occur in the above proportions on a given tree, or type 1 predominates, or types 2 or 3. There was no clear geographical pattern of distribution for these flower types, but in the northern range the frequency of 2-seeded berry-cones is greatest.

When mature the berry-cones range in size from 3 to 5 mm. in diameter. This variation in size shows an interesting geographic distribution. In the range of Red Cedar, with the exception of the Ozark Plateau and southwestward, the mature berry-cones normally measure 4 mm. across. Rarely, cones 3 and 5 mm. across are found on a particular tree. In the Ozark Highland, in Oklahoma, and in Texas east of the Balcones Escarpment, the berry-cones vary in size, but those measuring 5 mm. are most typical, and the 4-mm. and 6-mm. sizes are found in about equal abundance. One would expect to find a species well adapted to mesic habitats to express a major size modification in all its characters, as its range expands into more xeric environments. This is not so for the berry-cones, since their average size actually increases towards the southwest. The key to the significance of the variation in size lies in the behavior of this character in hybrid swarms where sizes range from one species to the other. The most significant fact is that the various patterns of size and shape of berry-cones occur with varied combinations of other characters of the two species, resulting in an inharmonic and heterogeneous population explicable only in terms of hybridization.

6. Seeds:

The seeds are good taxonomic characters in the genus, being mostly very different in the different species. They were not used in the scoring of populations, but they were often referred to simply as a check. In hybrid swarms especially, seeds were examined. In plants obviously intermediate in other characters, the seed varied between forms typical for each species.

The seed of *Juniperus Ashei* typically is 6 mm. long by 4 mm. wide and very sharply conical with an almost flat base. The base is covered with a conspicuous white hilum which may extend as much as one-third the length (2 mm.) up two opposite sides. The mature seed is invariably dark chocolate-brown except at the hilum. There may or may not be grooves along the sides formed by the pressure of resin canals as the ovules grow. Normally, there is one seed per fruit, occasionally two, the two-seeded condition being frequently accompanied by other interesting characters. Fruits with two seeds are most common in plants from

Ft. Worth to San Antonio, a region where hybrid swarms are common. Such seeds are not typical of *Juniperus Ashei* in color or hilum structure, since they are usually whitish to light yellow-brown and have very variable hilum shapes and sizes. Many seeds of one-seeded fruits found in this same region also vary considerably in color, size, shape, and pitting. Significantly, the variation is in the direction of *Juniperus virginiana.* The most common type of seed in a hybrid colony is one intermediate in size and in shape, with a few small bumps on the surface, and of a basic yellow-brown color thoroughly speckled with chocolate-brown everywhere except on the hilum. In such cases the hilum is usually very variable in size and shape (pl. 1).

In *Juniperus virginiana* the seeds are very small, usually 2 to 4 mm. long by 1½ to 3 mm. wide near the base. They are bluntly pointed and typically a very light slightly yellowish-brown. In the Ozark region the seeds are not only more frequently single, but also slightly darker, and show some variation in hilum size and shape. On the glades these characters are quite as variable as any of the others. In the hybrid swarms of southwestern Missouri the seeds are as have been described for similar situations along the Balcones Escarpment (Ft. Worth south to San Antonio).

Exserted seeds are quite common on specimens of *Juniperus Ashei.* Such seeds are much larger and more elongate than typical seeds; and from one-third to one-half their length is exposed at the apex of the fleshy berries. In every exserted seed examined insect detritus was found. In an infected tree the fruits are usually characterized by exserted seeds (a much rarer phenomenon in *Juniperus virginiana*). This condition is common in *Juniperus.* Every species which I have seen in the field has shown it to some degree. Martinez (1946) has reported this teratological condition in species of *Juniperus* in Mexico.

7. Terminal Whip:

The amount of long shoot growth on the secondaries (main branches) of mature plants is very different between specimens of *Juniperus Ashei* and *J. virginiana* of the same age. Plants must be at least mature before this character becomes useful in interspecific diagnoses. Youthful individuals of all species tend to have a great amount of long shoot growth per season. The long shoots were measured from the tip of the secondary back to the point where the shoot becomes woody. This is a somewhat arbitrary unit since the age of that position of the long shoot is slightly different for each species. However, this makes the character doubly good for our purposes, since it measures two differences at once. Two and sometimes three sub-regions of the terminal whip can be distinguished by the color and texture of the whip leaves. The region nearest the apex is, of course, the current season's fresh foliage. This is bright green and soft-succulent. Next is a length of yellowish tough foliage followed by one of brown woody foliage on which the whip leaves are still completely distinct. This constitutes all of the terminal whip; beyond this point the twig is grayish, woody, and sheathed with whip leaves whose bases are ruptured and in various stages of sloughing off.

In *Juniperus Ashei* the terminal whip is produced at a slower rate so that there is less whip length per year as judged by annual rings. The terminal whip always runs into the third year's growth. It is heavier, denser, and more rigid than that in Red Cedar. The leaves are ternate on these shoots except on some specimens in hybrid swarms.

Mature specimens of Red Cedar have much longer terminal whips than *Juniperus Ashei*, except in certain areas of the Ozark Plateau and in hybrid swarms. This whip runs into the second year (as judged by annual rings) but not the third year. Third year growth is well into the woody portion of the stem. The whip may have ternate leaves or decussate ones. The percentage of ternate foliage on the whips increases towards the southwest.

8. LATERAL WHIP:

The amount of long shoot growth on the tertiaries (lateral branches to the main ones) is quite different in typical plants of the two species. This character may only be used to contrast mature plants of nearly the same age. It is a variable character at best, but in young specimens it is too variable to be of any value. This character was utilized in the same way as the terminal whip. The lateral long shoot growth bearing distinct non-woody whip leaves was measured.

9. LEAVES:

There are three types of leaves common to most species of *Juniperus*, the SABINA section in particular. These are the acicular leaves characteristic of the *juvenile* foliage of seedlings, the elongate *whip* or long shoot leaves characteristic of the terminal and lateral extremities of the secondary and tertiary axes, and the small usually overlapping scale leaves whose bases are closely appressed to the *spur* or short shoot axes (see fig. 3).

Juvenile Leaves.—Both species are dicotyledonous. The seed-leaves are followed by acicular leaves which are the sole leaf type for three to five years or more, depending on the environment. Seedlings growing in a well-drained soil with no shading may develop adult foliage within three years. Those seedlings growing beneath other trees where shade is intense may not develop adult foliage for several years, and even then they will often retain some juvenile foliage indefinitely. Frequently in trees which suffer localized root injury, juvenile foliage is subsequently developed on portions of the plant, usually on the side of the injury. Such traumatic response is evidenced in new growth following a rock slide which does obvious injury to portions of the root system. Juvenile leaves vary in size rather markedly with different environmental conditions. In general, when juvenile foliage develops on a mature plant, its elements are proportionately smaller than those on seedlings.

In seedlings of *Juniperus Ashei* the juvenile leaves are normally 3-ranked, sometimes 4-ranked or rarely 5-ranked. A *typical* leaf has a sheathing base 2 mm. in length and fused with the axis, while the blade extends out from the axis at a nearly right angle to a length of 10–15 mm. The sheath and the widest part

of the blade, its base, are 1 mm. wide. The raised or humped gland is 1 mm. long and 0.3–0.5 mm. wide and is inserted half on the sheath and half on the blade. There are narrow stomatal lines on both surfaces on each side of the mid-vein. The mid-vein is conspicuous on the abaxial side and inconspicuous on the adaxial.

In *Juniperus virginiana* these leaves may be decussate but are usually 3-ranked, rarely 4-ranked. The sheath is 2–5 mm. long, and the blade is 8–12 mm. long. These leaves are 1 mm. wide along the sheath to a point on the blade nearly halfway to the leaf tip.

Whip Leaves.—These elongate leaves are even more different between the species than are the juvenile leaves. They are also quite different from juvenile ones. The differences are numerous but the most conspicuous one is in the ratio of sheath to blade. In juvenile leaves the blade is more than twice longer than the sheath, while in whip leaves the sheaths are longer than the blades.

In *Juniperus Ashei* a typical whip leaf is 1 mm. wide and has a sheath and a blade 4 mm. and 3 mm. in length, respectively. The abaxial gland is approximately 0.4–0.8 mm. in diameter and is a hollow sphere filled with a thin clear resinous liquid, seemingly a turpine complex. It is situated at the juncture of the sheath and the blade. The sheath usually has a thin keel extending to the base of the gland. The sheath and the blade of these leaves have teeth along the margins which are barely visible when magnified 12 times, but show up plainly at magnifications of 20–40 times. At higher magnifications these teeth are seen to be the result of occasional "spurs" or bends in certain of the epidermal cells of the margin. These large marginal cells are lined up at an angle with the longitudinal axis of the leaf.

In *Juniperus virginiana* a typical whip leaf is 1 mm. wide with a sheath and blade 9 mm. and 4–5 mm., respectively. The abaxial gland is a long hollow cylinder 2 to 5 mm. long and from 0.25 to 0.4 mm. in cross-section. However, on the back surface of the leaf this gland shows only as a thin line less than 0.2 mm. in width, no more than the width of a fine pencil mark. Most of the gland is on the sheath, but it extends along the blade a small portion of its length. The sheath is not keeled. The underneath surface of the blade has two longitudinal, fairly wide stomatal lines on each side of the very blunt mid-vein. The margins of the sheath and blade are smooth or very slightly undulate, never toothed. The marginal epidermal cells have their long axes nearly parallel to the longitudinal axis of the leaf and fit together smoothly with no out-jutting "spurs." The leaves are often covered with a white bloom which obscures the thin abaxial gland.

Spur Leaves.—These vary in size depending on their position in relation to the growing point from which they originated. In *Juniperus Ashei* a typical spur leaf has a sheath 1½ mm. long and a blade the same length. Where glands are present, they are round and raised and situated about ⅓ the distance from the base of the leaf. The sheaths are often keeled, and the blades are usually markedly humped. In *Juniperus virginiana* a typical leaf sheath is only 1 mm. long, while the blade

is 3 mm. long. The gland is elliptic and flat against the surface or slightly sunken and in the same position as described for *J. Ashei.*

In hybrid swarms many variations between the two leaf types occur. A plant may be found with every character of *Juniperus Ashei* except that it has a straight columnar habit and *no teeth* on the leaf margins. Specimens may have an intermediate leaf type, or both types together, or various intergradations of the two.

10. MICROSPORANGIATE STROBILI:

The pollen-bearing cone in *Juniperus* generally consists of four rows of shield-shaped sporophylls. The sterile part of the shield adjacent to the young sporangia grows downward and forms the mature peltate sporophyll. The sporangia are marginal and appear on the abaxial side at the base of the sporophyll.

In *Juniperus Ashei* the cone is made up of 12–18, usually 14, microsporophylls which have broadly rounded, abruptly acuminate, nearly mucronate tips and, like the leaves, have teeth on the margins. There is a small round flat gland approximately centered on the abaxial side. In Texas these cones may become visible late in December and usually have opened and shed their pollen by the middle of February.

In *Juniperus virginiana* the cone consists of 10–12, rarely 14, entire-margined sporophylls usually with blunt round apices. A conspicuous, somewhat elliptic gland is centered on the abaxial side of the sporophyll. These cones become recognizable as such in the Ozark region toward the last week of July and by early September contain mature microspores. Mathews (1939) reported that in North Carolina they are visible in August and pass the winter filled with microspores. According to Ottley (1909), in Massachusetts the cone develops much later and overwinters with microsporangia containing microspore-mother cells.

Where the ranges of the two species overlap, the whole cycle of reproduction also overlaps, so that the degree of open pollination which will be interspecific depends on local conditions for each individual. If conditions for pollination by either species are equally good, then Ashe Juniper pollen will dominate in the population. Ashe Juniper produces enormous quantities of pollen, while Red Cedar produces comparatively little. This fact is no doubt largely responsible for the difference in the extent of influence of the two species upon one another. Where there are large populations of both species in the same area, the bulk of the specimens of *Juniperus Ashei* show little effect of mixing while the specimens of *Juniperus virginiana* show a great deal. This fact complicates any attempt to draw conclusions as to adaptive or selective advantage in members of the hybrid swarms on the basis of the character combinations established there. In other words, there are a number of theoretically possible gene combinations which are not realized because of this tendency toward unidirectional flow of germ-plasm. This is not to say that the influence of *Juniperus virginiana* on *Juniperus Ashei* is ill-defined or slight in degree, far from it. Specimens of Ashe Juniper from along the Balcones Escarpment show quite extreme combinations of characters of the eastern species, as much so as in the other direction. However, the actual amount

or mass of the effect is much less to the southwestern species, since it so well outranks Red Cedar as a pollen producer.

In hybrid swarms there occur combinations of microsporophyll characters. The most evident trend is that specimens of *Juniperus virginiana* tend to have much more irregular-margined, occasionally some erose-margined sporophylls. There is also much variation in sporophyll shape, especially in relation to the apex characters.

11. Wood:

The heartwood of *Juniperus virginiana* is bright pink-red when fresh and fades to a dull brown-red. The pigment is reported to be very similar to that of *Sequoia*. Eccentric rings are very rare. In *Juniperus Ashei* the heartwood is a light dull brown. Eccentric rings are common. The heartwood to sapwood ratio is slightly greater in this species.

In eastern United States freshly cut cedar is completely homogeneous in heartwood color; in the Ozarks it is not. Brown heartwood increases in abundance as one approaches the Southwest. Often in Red Cedar trees from Ozark river bluffs and in multi-stemmed individuals, a dull brown heartwood is found, although in others it is a pink-red.

Study of Variation

It was necessary to find dependable characters which would indicate as accurately as possible the degree of hybridization between the two species. This required a survey of the variation within each species in areas where contamination was least likely. Characters were then chosen with regard to their degree of independence, variability, and difference. These were to be contrasted in population studies over as much as possible of the total ranges of both species.

The method of determination of suitable characters was inevitably laborious. Ideally, complete genetic analyses of the behavior of characters are needed in order that character correlations may be carried on with complete confidence. On superficial examination, it often appears that multiple-character correlations make something difficult and messy out of something easy. Good unit characters are seldom characteristic of species. Many apparently good species are differentiated only by contrasting several (usually quantitative) characters. Since multiple-factor characters are the basic genetic material in population dynamics, it seems necessary to employ multiple correlations in order to demonstrate the nature of differentiation within the population. The analysis of the behavior of a single character in a population can only lead to conclusions concerning that single character. The presence of a cline of variation which demonstrates intermediacy is not evidence that the intermediates are the result of hybridization. Hybridization can be inferred only from variation patterns which demonstrate recombinations of characters. Combinations of characters are the clues which rule out other conditions causing intermediacy—environmental modifications, differential selection of intraspecific gene patterns, divergence preceding isolation.

The first problem, environmental modification, may be solved by experiment or perhaps by careful observation in the field. The second, differential selection, is not so easy when only a single character is employed. Intermediate environments may select intermediate characters, but differentially; that is, some characters may be selected more strongly than others; thus a single character study is not so reliable in demonstrating the cause or causes of variation. The marginal waifs and transition-zone variants show up markedly when multiple correlates are utilized. The third factor, divergence preceding isolation, involves timing. How can one tell, from single character clines, which end of the variation spectrum he is observing? Is he observing divergence consequent to isolation or allopatric hybridization? The multiple-correlation technique offers greater security in two ways: after one roughly determines the behavior of several characters under different environmental conditions, he may study their synthetic behavior, which demonstrates whether they have the structure of recombinations and how well they are linked, or whether they constitute continuous clinal gradients. The multiple correlation scheme is, in brief, a much better description of what the organisms of a population are doing.

The subtleties of correlation suggested above are not so serious in studies between two species well differentiated morphologically and ecologically. Interspecific variations are usually not so cryptic as intraspecific ones. I repeat, that if introgression is occurring in *Juniperus* it should give evidence in four ways: (1) that the species in question will hybridize. (This may be experimental verification or the presence of hybrid swarms where the species occur together); (2) that there are recombinations of the characters from the species in question; (3) that when characters of one species occur in the other they become progressively more "dilute" away from the region of hybrid swarms; and (4) that the characters which differentiate the two species should be at least slightly correlated throughout the area of introgression.

It is only in an analysis of the patterns of recombinations of more than one character, preferably of many characters, that introgression can be inferred. Even multiple correlations may not constitute proof of introgression but are the working basis for an hypothesis which may subsequently be tested by experiment. The experiments must meet two general requirements: (1). They must indicate through controlled breeding that the morphological and/or physiological patterns which arise by crossing species are similar to the situations found in nature. (2). They must show that these patterns cannot in like manner be produced by other factors—specifically, direct modification through environmental action.

In this study it has been possible to check only the second general requirement, since this work on *Juniperus* is inductive and deductive with only a small amount of strictly experimental evidence. The conclusions, therefore, are products of inference and in the rigid sense of scientific discipline may not be taken as proof.

Since morphological characters may vary a great deal in sensitivity to environmental effects and likewise in their genetic stability, it was desirable to select those which would be the most sensitive index to ecological differentiation and at the same time indicate possible ways in which their potential of variation was initiated. It would do little good to use characters for contrast which are so stable that under natural conditions only very slight variation occurs; in consideration of the antithetic situation, extremely morphoplastic characters are also objectionable. Most characters of *Juniperus* are intermediate in these respects, possibly with a slight edge toward morphoplasticity. Both types of characters were available and both were used for a special reason. Those which fluctuated somewhat were separated from the more stable ones by studying the morphology of hundreds of individuals throughout the range of the two species and by ascertaining the behavior of these characters in horticultural varieties throughout the range of *J. virginiana*. A character was considered fluctuating if it expressed a high degree of variability. Conversely, a character was considered stable if it remained constant throughout the range of the species. This particular part of the investigation was made only in those areas where the two species were far from contiguous.

If one could show evidence of recombinations of the fluctuating characters where the variance of the character in any particular individual was no greater or less than could be expected in either species in the same area, while the stable characters were varying within the individual much more than could be expected, then it could be inferred that this variation was the result of recombinations through hybridization.

Individuals in natural populations at the Missouri Botanical Garden Arboretum, Gray Summit, Missouri, were studied at first to determine what characters of *Juniperus* would be most suitable as an index to purity or hybridity. Later, these characters were extensively checked in areas known to have homogeneous (concordantly varying) *Juniperus virginiana,* and again in areas known to have typical *J. Ashei.* The following six characters were analyzed in detail as to the degree of variation from one branch to another on a single tree, their relative independence, variability, and significance as an index of difference:

1. Ratio of gland length to gland width.
2. Length of a typical terminal whip leaf.
3. Length of terminal whip at the apex of a typical secondary shoot.
4. Length of lateral whip on the same secondary shoot.
5. Per cent of decussate spur shoots on the secondary shoot.
6. Leaf margins, scored as smooth (S), denticulate (D), or intermediate (I).

The characters also had to be checked for their seasonal variability. Of the characters discussed under "Comparative Morphology," the six listed proved to be most convenient and dependable. The sex was recorded in order to check for any possible correlation with the other characters. In so far as possible the diameter of mature berry-cones was recorded. Seed characters were carefully studied for all populations and proved to be very stable. Unfortunately, seed characters were

far from convenient to use as a measure, but they were used as a parallel to the others as an indicator of hybridization.

Measurement of Characters

The measurement of these six characters involved population sampling over a considerable area. For convenience, each sample compilation will be given a group number for each species.

Juniperus Ashei:

Group A-I.—A survey of the general area was made. More than 200 specimens were measured by traversing the Edwards Plateau of Texas (Comanche Series of the Cretaceous) from Junction to Garner State Park to Boerne and thence to the east of the Central Mineral Region and north to Stephenville.

Group A-II.—A survey was made of regions where *Juniperus Ashei* is found growing in the vicinity of *Juniperus virginiana.* This was along the base of the Balcones Escarpment (Gulf Series of the Cretaceous) from New Braunfels to

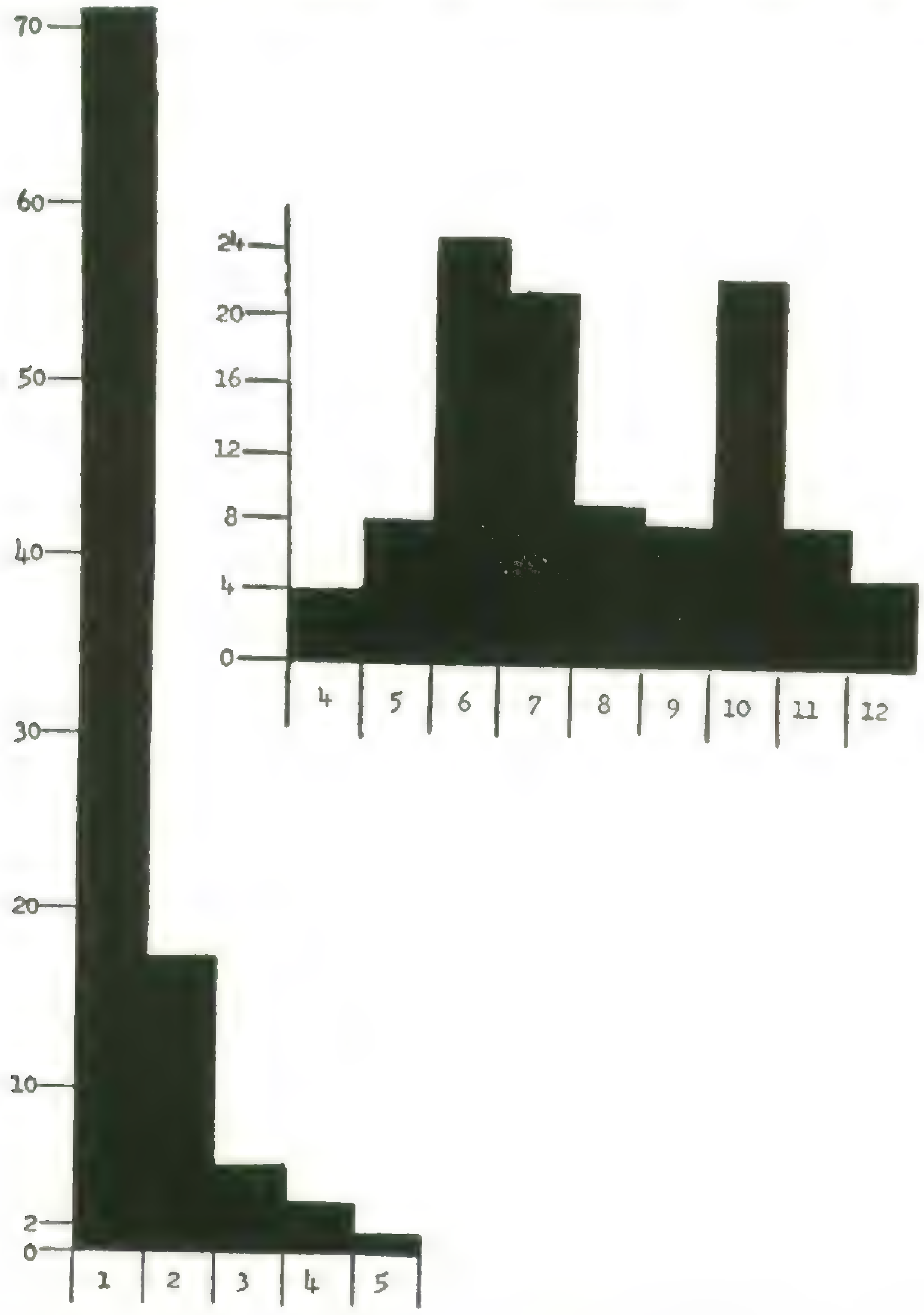

Fig. 4. Ratio of whip-leaf gland length to width from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency.

Austin to Georgetown to Waco. Twenty-five plants were measured in populations near the cities named.

Group A-III.—Twenty-five specimens in the Arbuckle Mountains, Murray County, Oklahoma, were measured.

Juniperus virginiana:

Group V.—A survey was made of the regions where this species grows as a tall forest tree removed from other species. One hundred plants were measured from populations of southern Indiana, Kentucky, and Virginia, respectively.

When the six characters in groups A and V were compared, each was repeatedly found to be useful as an index of morphological affinity; in other words, an individual juniper may be fairly exactly placed in terms of specific reference to these characters. Graphs for each character demonstrate the differences between the A and the V groups (see figs. 4–8).

1. Ratio of Gland Length to Width:

This value had a constant value of 1 in Group A-I. In Groups A-II and III the ratio varied from 1 to 5: 80 per cent had a value of 1; 10 per cent, 2; 5 per cent, 3; 3 per cent, 4; and 2 per cent, 5. The frequency of the higher values increased northeastward.

In Group V the values for the ratio varied from 4 to 12. The total curve for 100 specimens was bimodal. The primary mode was 6 while the secondary mode was 10. The bimodality was contributed by values of a single population from Virginia, which were the highest of all measurements made except those for southern Michigan and Pt. Pelee, Ontario, where *Juniperus virginiana* grows in the same habitat as *J. horizontalis*, which also has a mode of 10 for this character. The median was 7 and the mean 6.9 (see fig. 4).

2. Length of Typical Terminal Whip Leaf:

Originally, this character was measured by taking the total length of all the terminal whip leaves and dividing by the number of them. Later it was found that the average length of three leaves equally spaced on the whip shoot was satisfactory.

In Groups A-I, II, and III the values ranged from 2 mm. to 14 mm. with the mode at 4 mm., the median at 5, and the mean at 5.5. Beyond the value 9 there were only 3 measurements of 10, 3 of 11, and 1 of 14. The values had a very definite geographical pattern of distribution, for the extreme measurements, or those more characteristic of *Juniperus virginiana*, were found only in regions where the two species occur in proximity. Values from 2–6 were in Group A-I; values from 7–14 were in Groups A-II, III. The range of values in Group V was from 4 to 16 mm., with the mode at 8 mm., the median at 9 mm., and the mean at 8.95 mm. From Virginia toward the Shawnee Hills there was a tendency toward slight reduction in leaf length. (See fig. 5 for a graphic representation of the whole.)

3. Length of Terminal Whip:

This character was measured as described in the section on "Morphology," from the apex back to the point where the shoot is obviously woody. Even though this

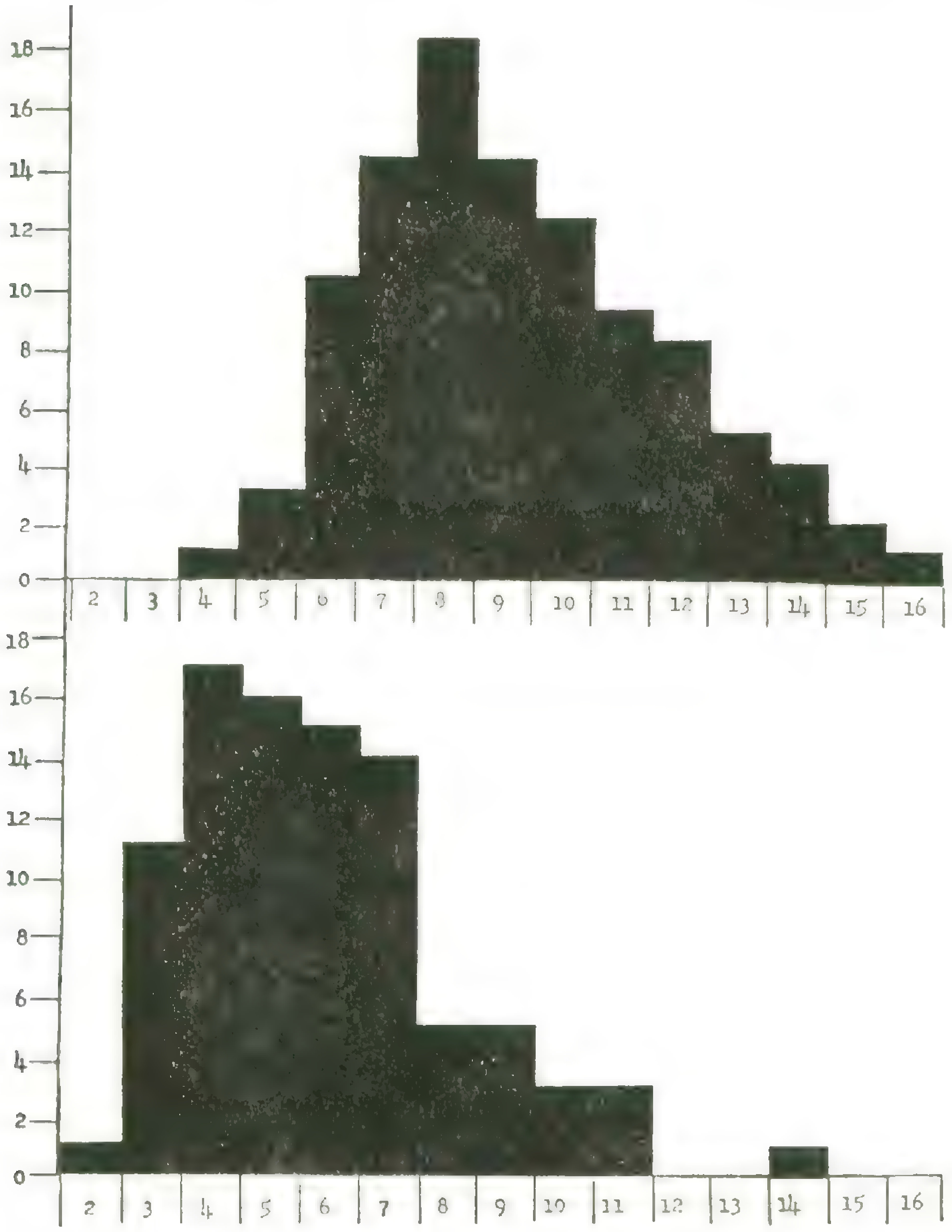

Fig. 5. Length of whip leaf from 100 specimens of *Juniperus virginiana* (above), and 100 specimens of *J. Ashei* (below). Ordinate values represent frequency; abscissae, millimeters.

growth does not represent exactly the same age in each species, the length difference was great enough to render the character valuable. As evidenced by ring transition, a section of *Juniperus Ashei* at any point back from the tip was always slightly older than a comparable point in *J. virginiana.*

In *Juniperus Ashei* the range of variation was from 0 to 200 mm. of terminal whip while the mode was at 40 mm., the median at 60 mm., and the mean at 62 mm. This character was the most variable of all those measured in this species. In *J. virginiana* the range of variation was from 30 mm. to 230 mm. of terminal whip while the mode was 80 mm., the median 120 mm., and the mean 118.8 mm. (See fig. 6.)

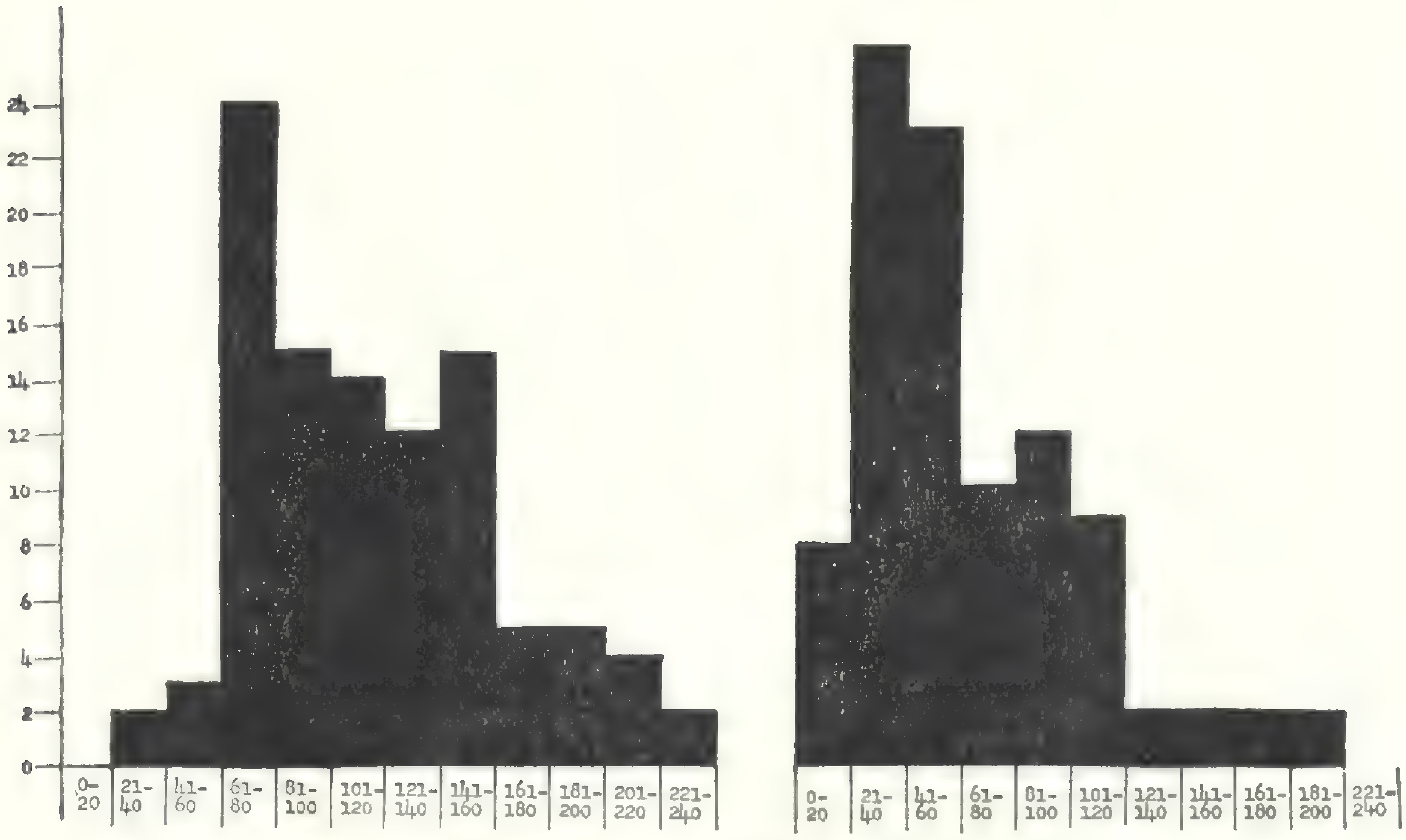

Fig. 6. Length of terminal whip from 100 specimens of *Juniperus virginiana* (left), and from 100 specimens of *J. Ashei* (right). Ordinate values represent frequency; abscissa values, millimeters.

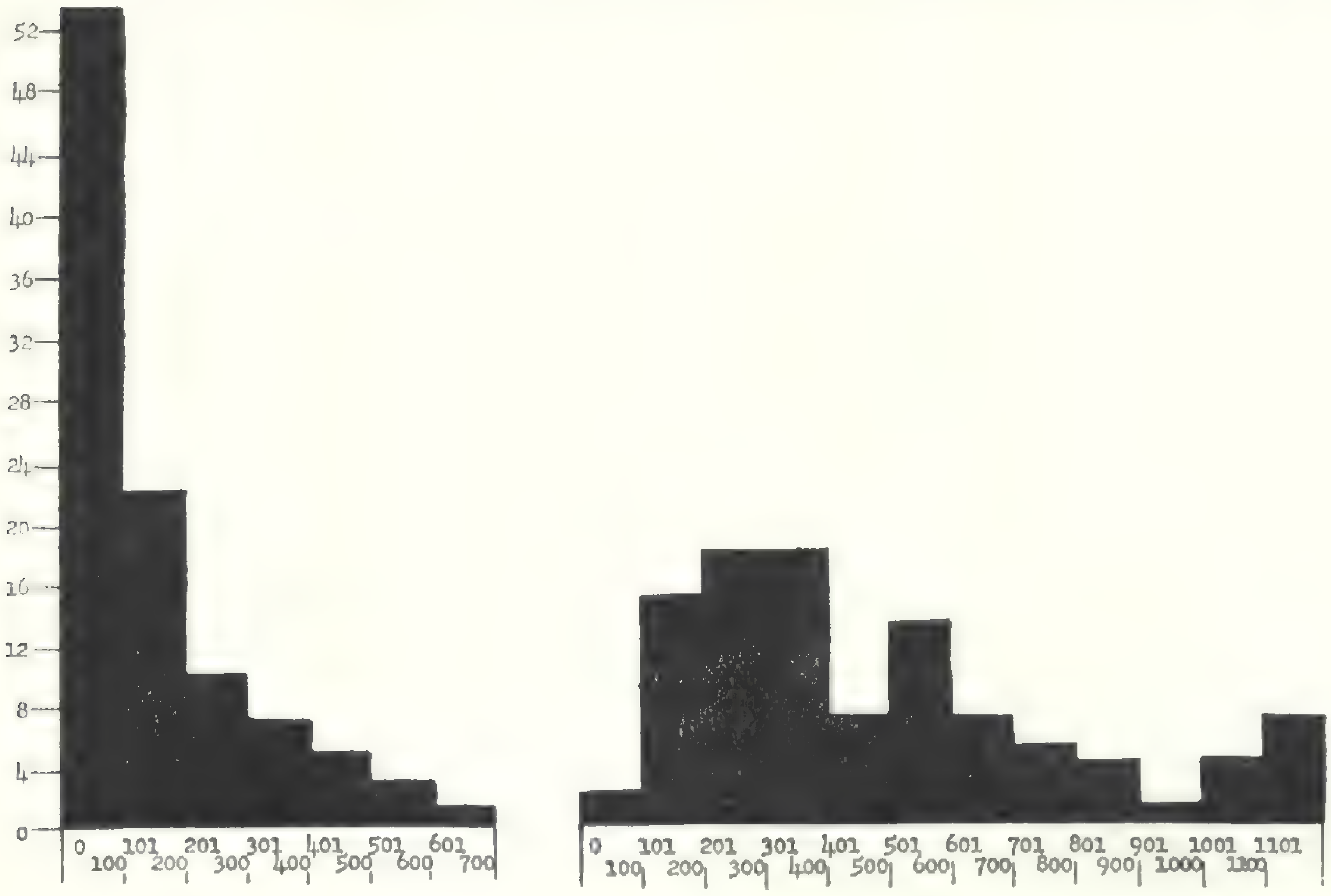

Fig. 7. Length of lateral whip on the secondaries from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency; abscissa values, millimeters.

4. Length of Lateral Whip on the Terminal Shoot:

This was measured on the same shoots, the secondaries, which bore the terminal whip. These shoots were arbitrarily collected in lengths of 45 cm. The measurements of lateral whip were found to vary from 0 to 1200 mm. With such a tremendous range it was thought advisable to group the measurements, and they were therefore tabulated in units of 100 mm. (fig. 7).

In *Juniperus Ashei* the value with the greatest frequency was 0, the median value was 80 mm., and the mean 90 mm. The range was from 0 to 500 mm. In *J. virginiana* the median value was 410 mm., the mean 390 mm., and the range was from 30 to 1200 mm.

5. Per Cent of Decussate Spur Shoots on the Terminal Shoots:

This involved the determination of the per cent of the spur shoots on the terminal whip which had leaves in decussate arrangement. Species of *Juniperus* tend to have ternate leaves on the spurs of the terminal whips, but some species have all ternate spurs so situated while others have a variable amount.

Juniperus Ashei typically has the ternate leaf arrangement, as evidenced by the fact that in Group A-I no decussate spurs were found. Groups II, III were not characterized completely by the ternate condition, but instead expressed the trend of increased percentage of the decussate arrangement northeastward. The range in Groups II and III was from 0 to 30 per cent (decussate).

In *Juniperus virginiana* the range of values was from 10 to 100 per cent (decussate); the average as depicted by the median and the mode was 40 per cent; and the mean was 44 per cent (decussate). In this species the spurs on the terminals of an average plant are about one-half ternate and one-half decussate, while in *Juniperus Ashei* they are always ternate except where the two species are in proximity (see fig. 8).

6. Leaf Margins:

The sabina section of *Juniperus* may be separated into two groups on the basis of the presence or absence of teeth on the margins of the leaf. Engelmann (1877) was the first botanist to indicate the value of this character in separating species in the sabina section, but he admitted that considerable magnification was necessary to render it visible. He wrote, "the edges of the leaf are rarely entire, mostly delicately denticulate, or irregularly fringed with minute, corneous, often curved processes." *Juniperus Ashei* falls into the group with teeth, while *J. virginiana* is in that without teeth. The nature of the margins was discussed in the section on "Comparative Morphology."

From collections represented by Groups A-I, II, III, and Group V, leaves were selected from comparable parts of each specimen and stripped of upper epidermis including the margins. These epidermal peels were stained in aniline blue and mounted in balsam to be studied with respect to marginal dentation. Group A sections displayed the denticulate condition, although an occasional specimen in Groups II and III had fewer teeth than typical, and the cells tended to be situated at a lesser angle to the longitudinal axis of the leaf. In Group V there were no

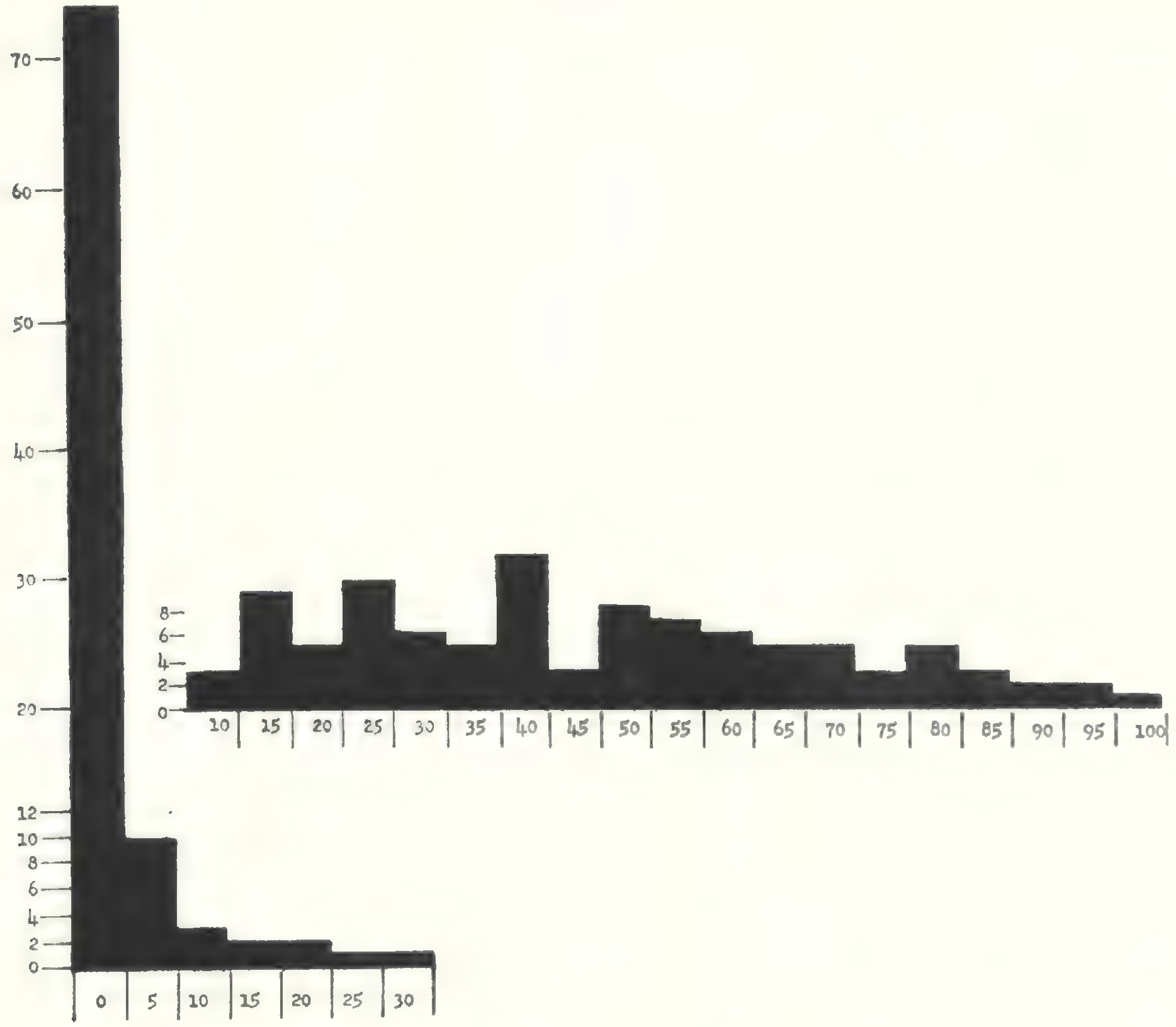

Fig. 8. Per cent of decussate spurs on the secondaries from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency.

teeth, and the marginal cells were aligned nearly parallel to the mid-rib. This character was then to be used and scored as D (denticulate), I (intermediate, arbitrarily if 2–4 teeth were visible), S (smooth or entire margins). Then the relative sizes of the epidermal cells of the two species were studied. These data indicated cell size to be a good species difference. There was no overlap in cell size between the two species. *Juniperus Ashei* had appreciably larger epidermal cells which were nearly isodiametric in surface view. The smaller cells of *J. virginiana* were columnar in surface view and nearly always twice or more longer than wide. In some hybrids the cellular pattern was so extremely variable that oddly shaped leaves, which were thought to be a result of upset growth patterns, were common.

Variability of the Characters

In order to be confident of the index-value of these six characters, it was necessary to learn how much variation might occur in any one of them on a single tree. An intensive study was made on individual plants of *Juniperus Ashei* near Kerr-

ville, Texas, and of *J. virginiana* at the Missouri Botanical Garden Arboretum. This population of Red Cedar was not native material, but of stock brought from Virginia and planted under natural conditions. Intra-individual variation was somewhat less in the southwestern species than in the eastern type of Red Cedar at the Arboretum. In neither example was the degree of variation sufficient to cloud the interpretation of variation of the whole population. Individuals of a bluff population native at the Arboretum were found to show more intra-individual

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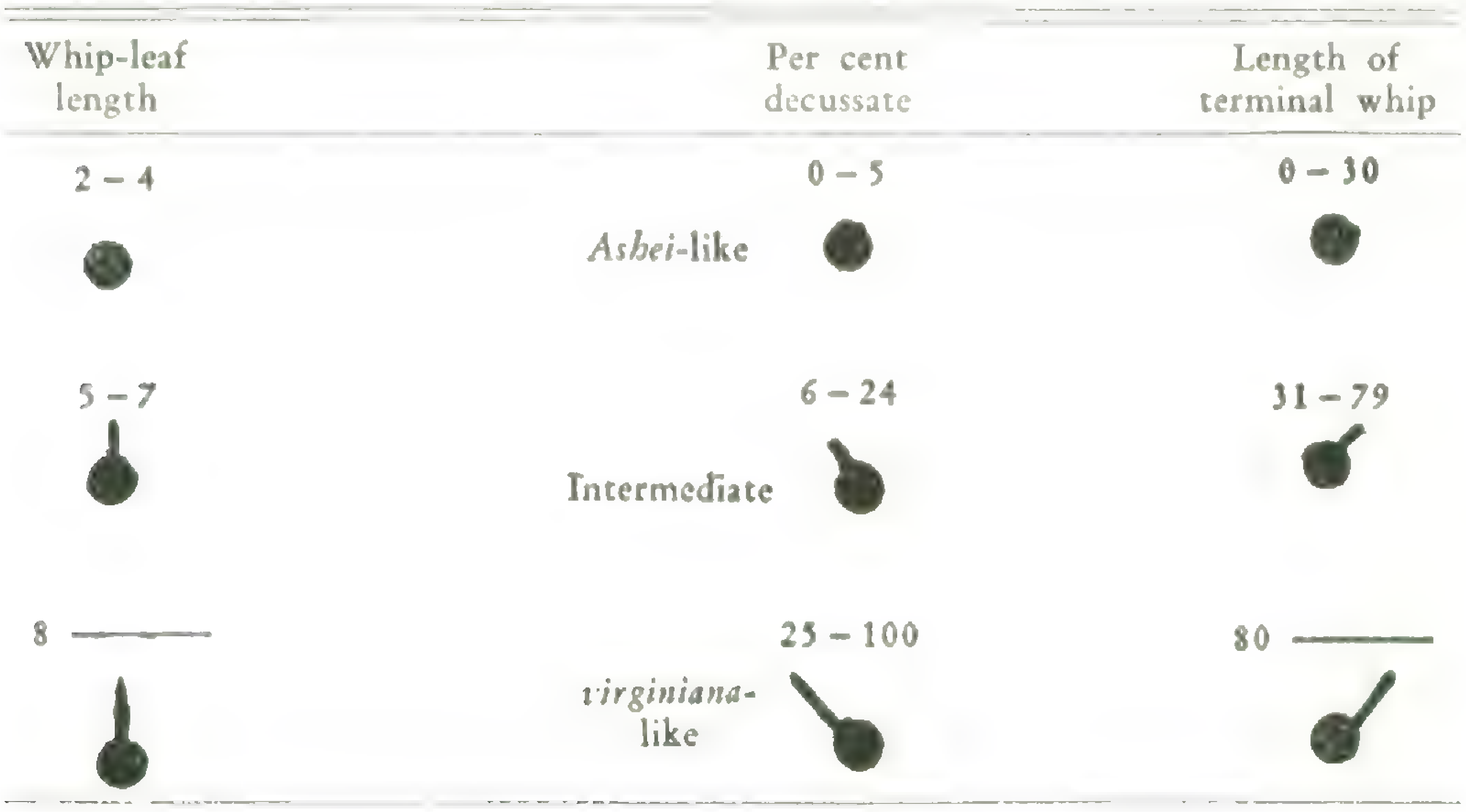
EXPLANATION OF PICTORIALIZED SCATTER-DIAGRAM SYMBOLS IN FIGS. 9–17

Ordinal character is gland length-width ratio; abscissal character is length of lateral whip.



Figs. 9–11. Locations represented by scatter diagrams 1–18, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2–3; "Pure" *J. virginiana*, 8–12. Explanation of symbols above.

Fig. 9—

1. Kerrville, Kerr County, Texas .... Population mean 2.13
2. Arbuckle Mountains, Murray County, Oklahoma 2.28
3. Bexar County, Texas 3.72
4. Roaring River State Park, Barry County, Missouri 3.96
5. McVey Knob, Ozark County, Missouri 4.12
6. McVey Cliff, Ozark County, Missouri 4.20

Fig. 10—

7. Bald Knob, Taney County, Missouri 4.28
8. Wichita Mountains, Meers, Comanche County, Oklahoma 4.45
9. Austin, Travis County, Texas 4.62
10. Brownbranch, Taney County, Missouri 4.96
11. Lake of the Ozarks, Camden County, Missouri 5.08
12. Fourche a du Clos, Ste. Genevieve County, Missouri 5.16

Fig. 11—

13. Gray Summit Cliff, Franklin County, Missouri 5.20
14. Gray Summit, Cedar Hill, Franklin County, Missouri 5.48
15. Fremont, Nebraska 5.71
16. Nankipoo, Tennessee 5.76
17. Noble, Cleveland County, Oklahoma 6.00
18. Jasper, Newton County, Arkansas 6.00

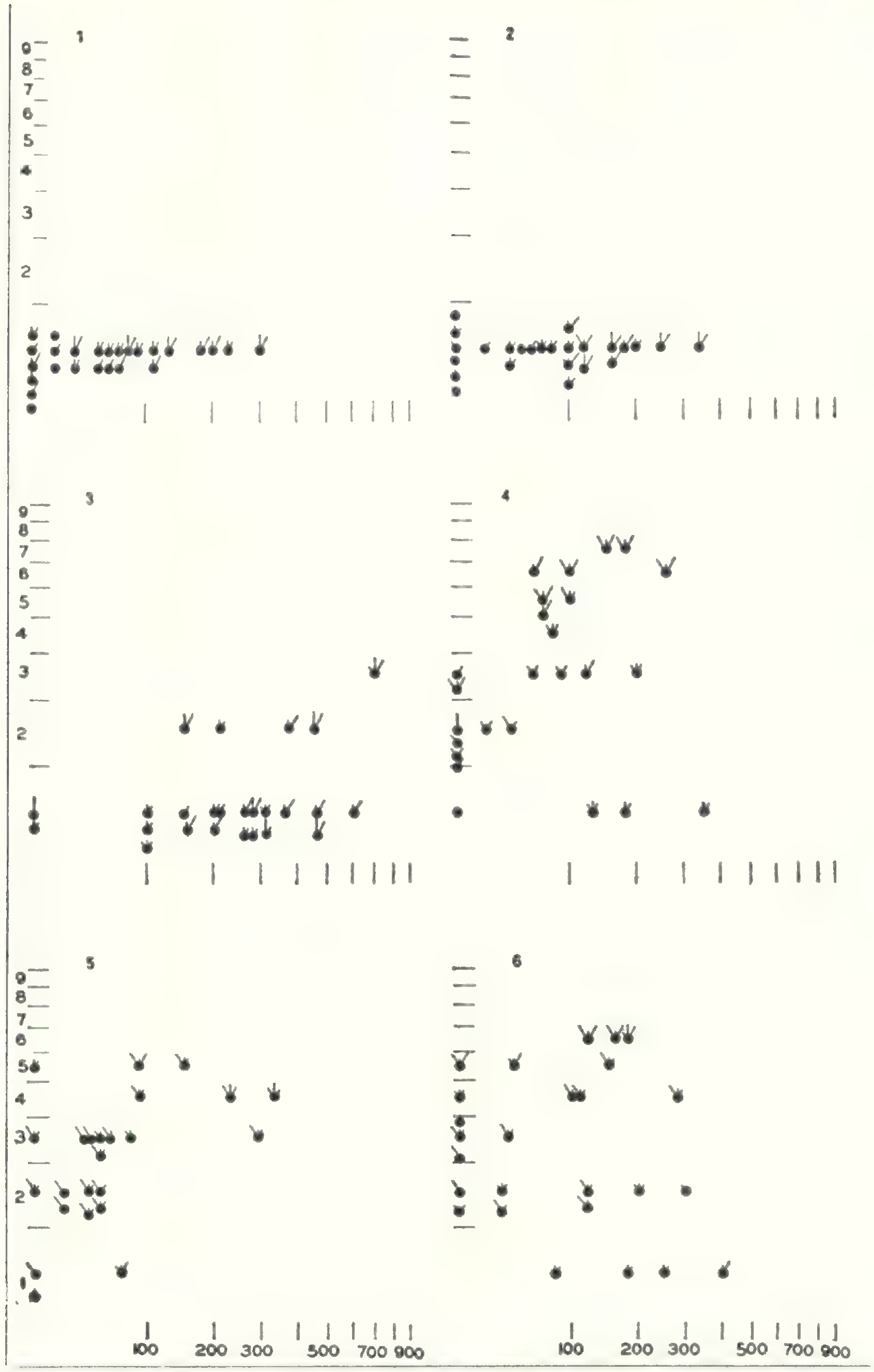


Fig. 9

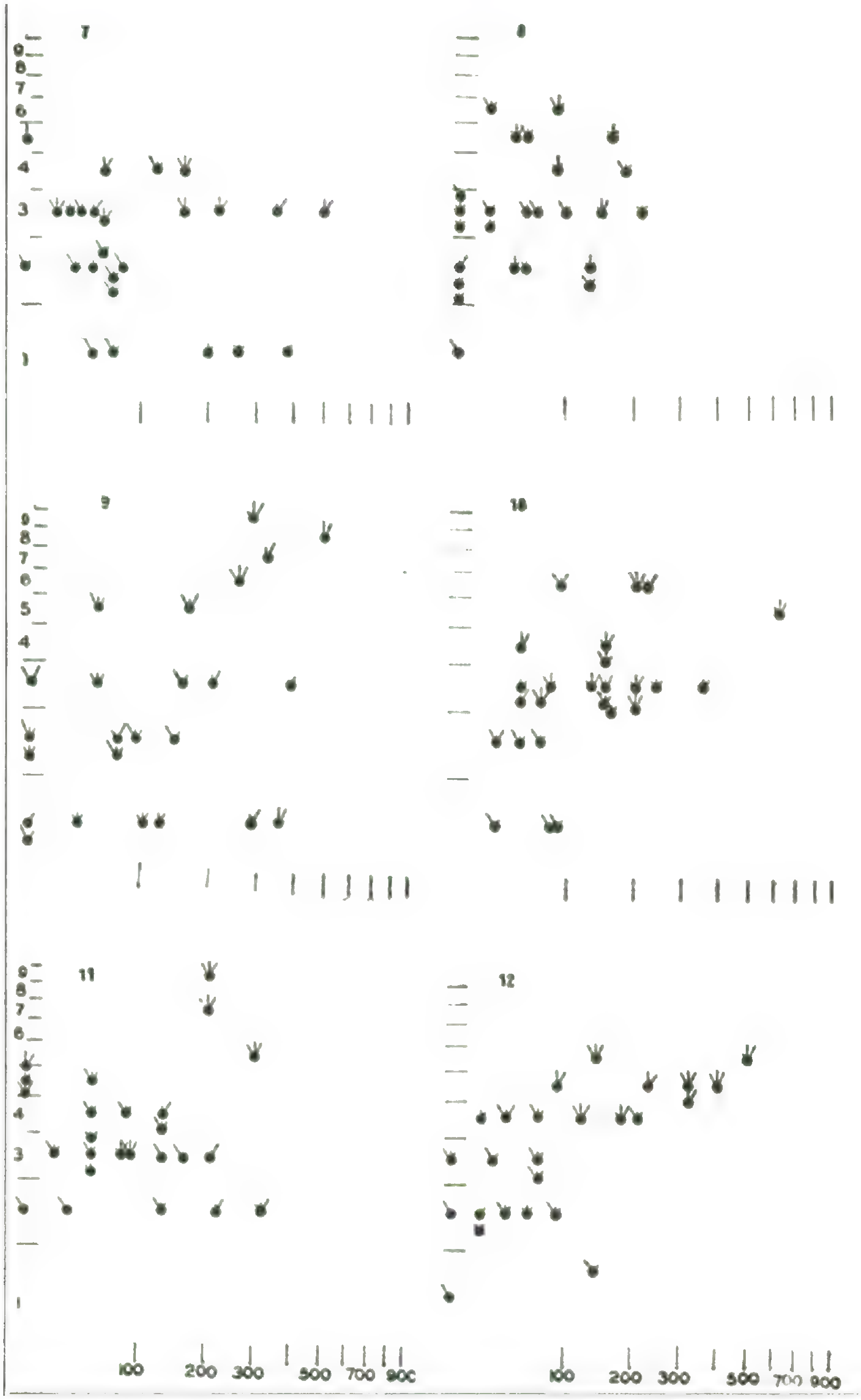


Fig. 10

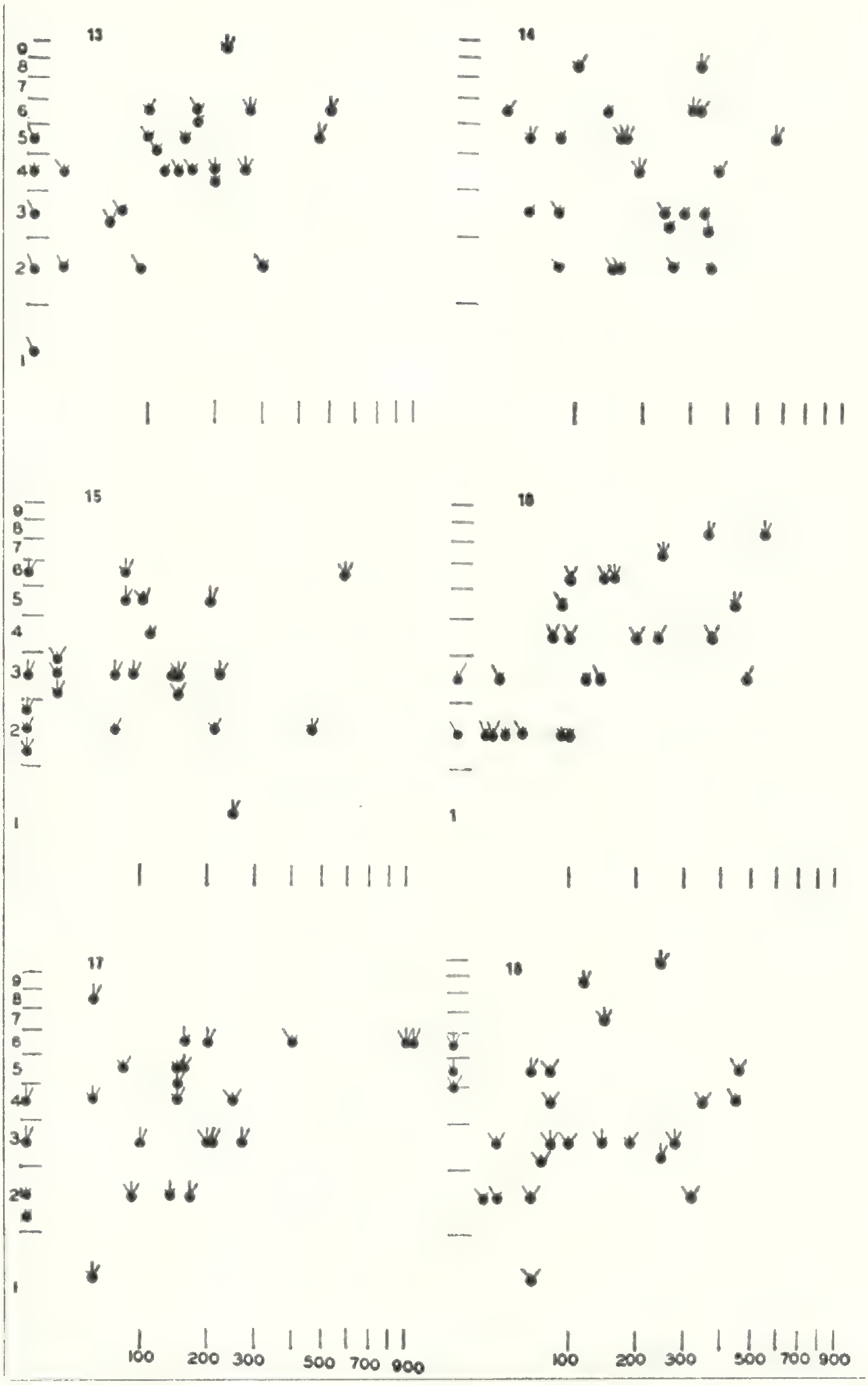


Fig. 11

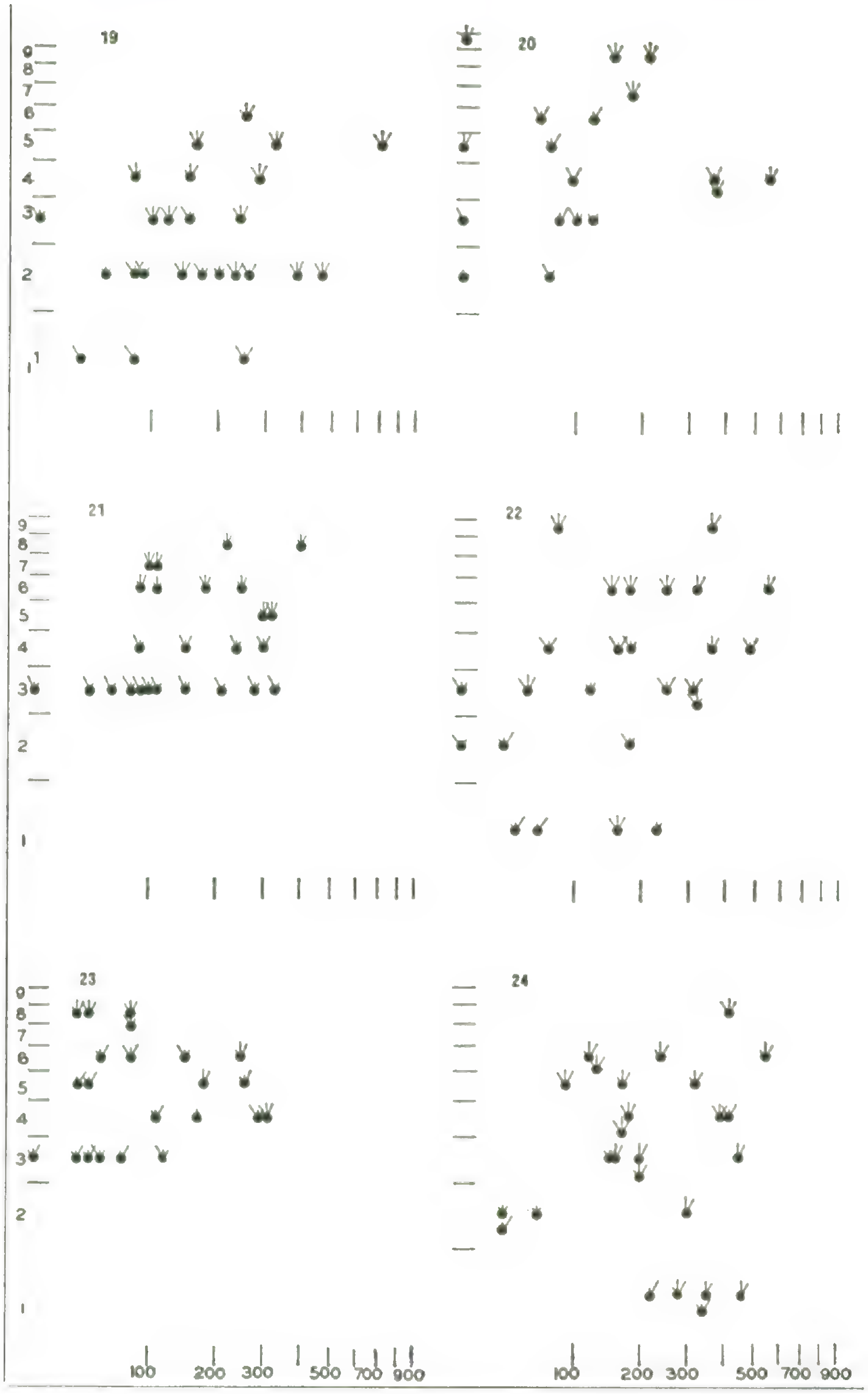


Fig. 12

variation than those from gently sloping hillsides. The variation in these hillside specimens was greater than in bluff populations along the Illinois and the Mississippi rivers.

The variability of individuals of the bluff and glade populations made it necessary to determine the reliability of the methods for recording the intermediacy and the variability of whole populations. By actual test it was found that the methods gave repeatable results and were therefore scientifically valid. Repeated scorings of labelled populations gave the same general population picture, even though the values for individual trees were not always precisely the same in each diagram. Repeated samplings of the same population by one individual, or independent samplings by two observers, produced essentially similar population diagrams.

The program was complicated by the great intra-individual variability of certain of the specimens, particularly those in the areas of intensive introgression. Though the phenomenon has never received critical study it is well known to various students of hybridization that hybrids, both in artificial and natural populations, may have greater intra-individual variation as well as the greater inter-individual variation which is known to be so characteristic. It might be argued that this greater lability of the Ozark trees was the result of the environment in which they were growing. In answer to this, one might point to the Ashe Junipers themselves. Though growing in an environment which is similar to the Ozark

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Figs. 12–14. Locations represented by scatter diagrams 19–36, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2–3; "Pure" *J. virginiana*, 8–12. Explanation of symbols on page 40.

Fig. 12—

19. Arpelar, Pittsburg County, Oklahoma	Population mean 6.04
20. Indian Springs, Crawford County, Missouri	6.10
21. Olivehill, Carter County, Tennessee	6.16
22. Wilburton, Latimer County, Oklahoma	6.20
23. Caddo Canyon rim, Caddo County, Oklahoma	6.24
24. Platt National Park, Murray County, Oklahoma	6.31

Fig. 13—

25. Poteau, LeFlore County, Oklahoma	6.36
26. Pilot Grove, Iowa	6.40
27. Scott County, Missouri	6.52
28. Ludwig, Johnson County, Arkansas	6.64
29. Talihina, LeFlore County, Oklahoma	6.84
30. Columbus, Kansas	7.13

Fig. 14—

31. Mt. Pleasant, Iowa	7.15
32. La Grange, Lewis County, Missouri	7.20
33. Butts, Crawford County, Missouri	7.32
34. Paducah, McCracken County, Kentucky	7.34
35. Raleigh, Wake County, North Carolina	7.44
36. Rosedale, Jersey County, Illinois	7.60

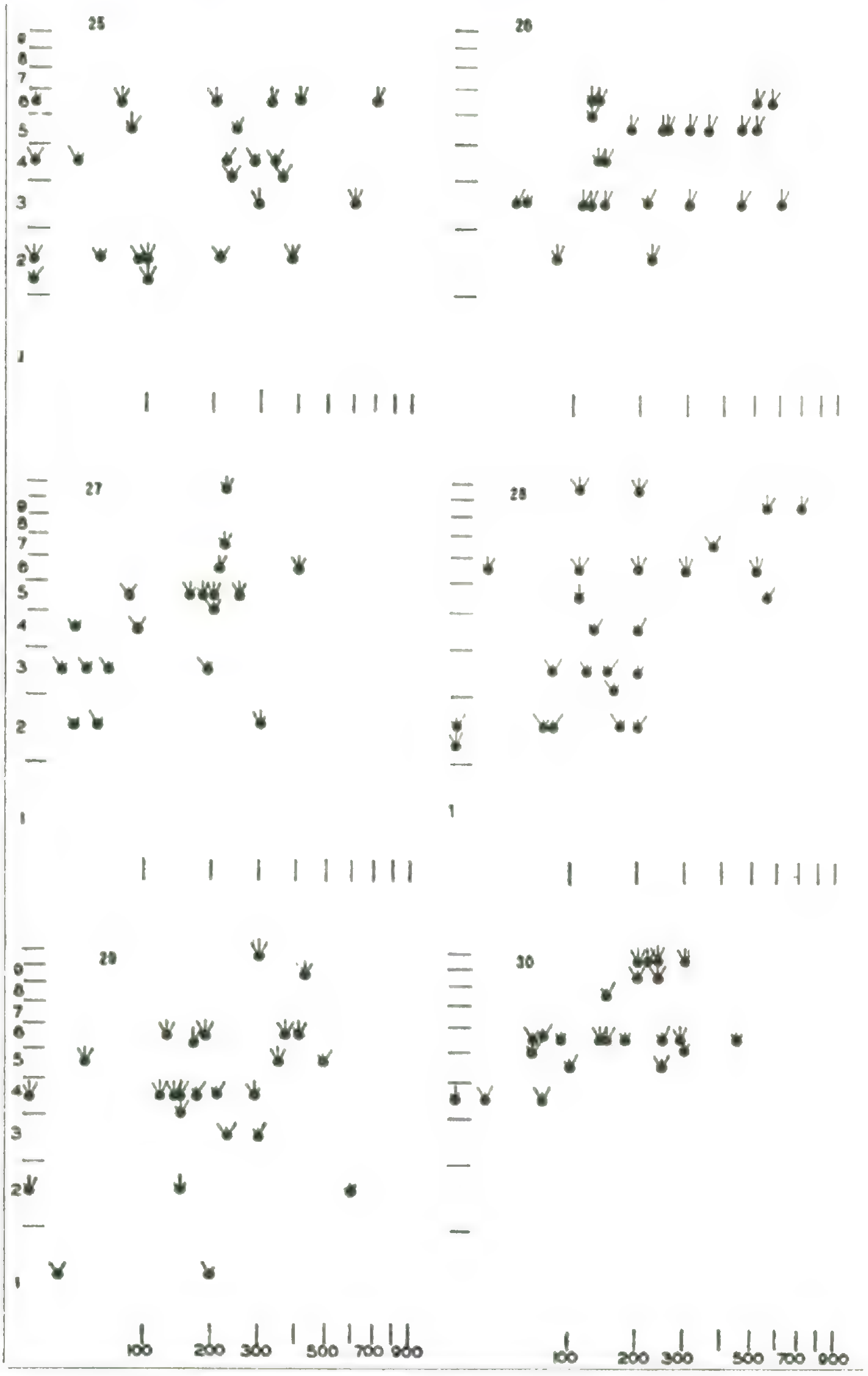

Fig. 13

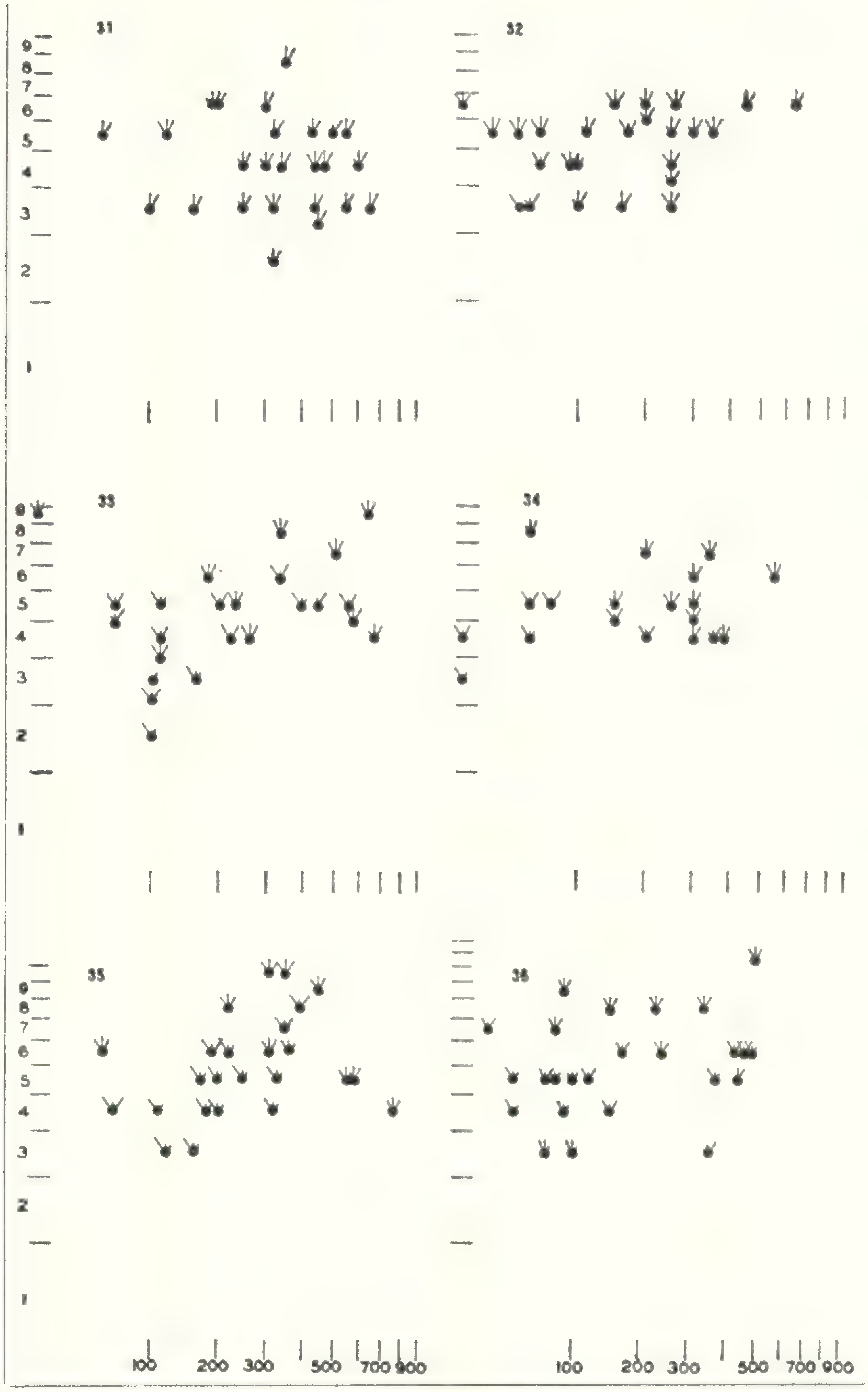

Fig. 14

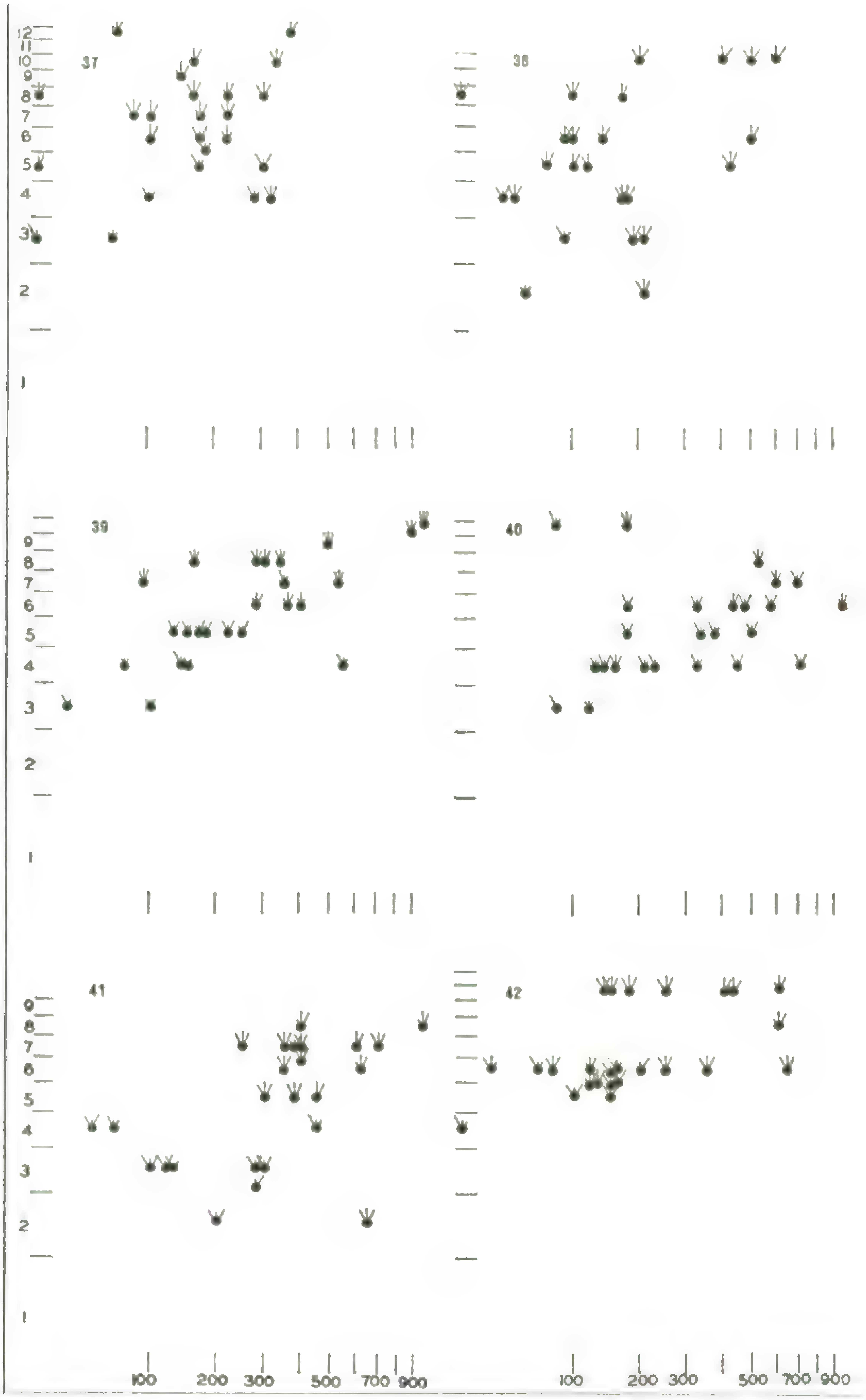

Fig. 15

glades and bluffs, the "pure" Ashe Junipers exhibit no more intra-individual variability than do the "pure" specimens of Red Cedar from Tennessee. In other words, the variability patterns of the Ozark junipers do not follow a logical development in terms of the influence of environment alone. When all the data are integrated and juxtaposed on their geographical backgrounds, it is obvious that the mixing of germ-plasms plays the important role in determining the heterogeneous nature and the biotypic differentiation of Red Cedar in the Ozark region and southwestward.

To check the effect of environment, climate particularly, a study was made of *Juniperus virginiana* var. *Canaertii* from Oklahoma to eastern Michigan. This variety is usually propagated by grafting young seedlings onto native Red Cedar stock. A population at the University of Oklahoma Nursery in Norman was scored, one in St. Louis, Mo., and one in Ann Arbor, Mich. The scatter diagrams (fig. 17, Populations 52, 53, 54, composed of individuals grafted onto root systems of local Red Cedar stock) illustrate the extreme homogeneity. However, specimens were also scored which were grafts onto Chinese Arborvitae *(Thuja orientalis)* root systems. These pictograms were identical with the ones illustrated. It would be wrong to assume that only one horticultural variety should be an index to environmental effects on the species, but several well-known varieties were carefully examined in nurseries and arboretums in order to satisfy that point.

Population Study

The patterns of these six characters having been found to be suitable indications of specific affinity without too much clouding through environmental modifications, population sampling was undertaken on a large scale. The minimum number of 25 specimens to be studied per population was set for two reasons: (1) The diagrams for 25 specimens studied at the Missouri Botanical Garden Arboretum produced the same picture as those for 50 specimens; (2) The paucity of mature specimens in a few areas (regions where a very high percentage of the land was under cultivation) necessitated the utilization of reasonably small samples.

During this phase of the study, specimens from 54 populations, representing 1,350 individuals, were measured for the six characters listed; sex and berry diameter were recorded; and the habitat was briefly described. These data and mass collections from all these areas are filed at Cranbrook Institute of Science, Bloomfield Hills, Mich. The specimens were collected in the area from Virginia

Fig. 15—

37. Wichita Mountains, Mt. Scott, Comanche County, Oklahoma................Population mean 7.60
38. Caddo Canyon floor, Caddo County, Oklahoma 7.70
39. Spring Hill, Maury County, Tennessee 7.76
40. Baker's Grove, Davidson County, Tennessee 7.80
41. Carbondale, Williamson County, Illinois 8.20
42. Craig County, Virginia 8.30

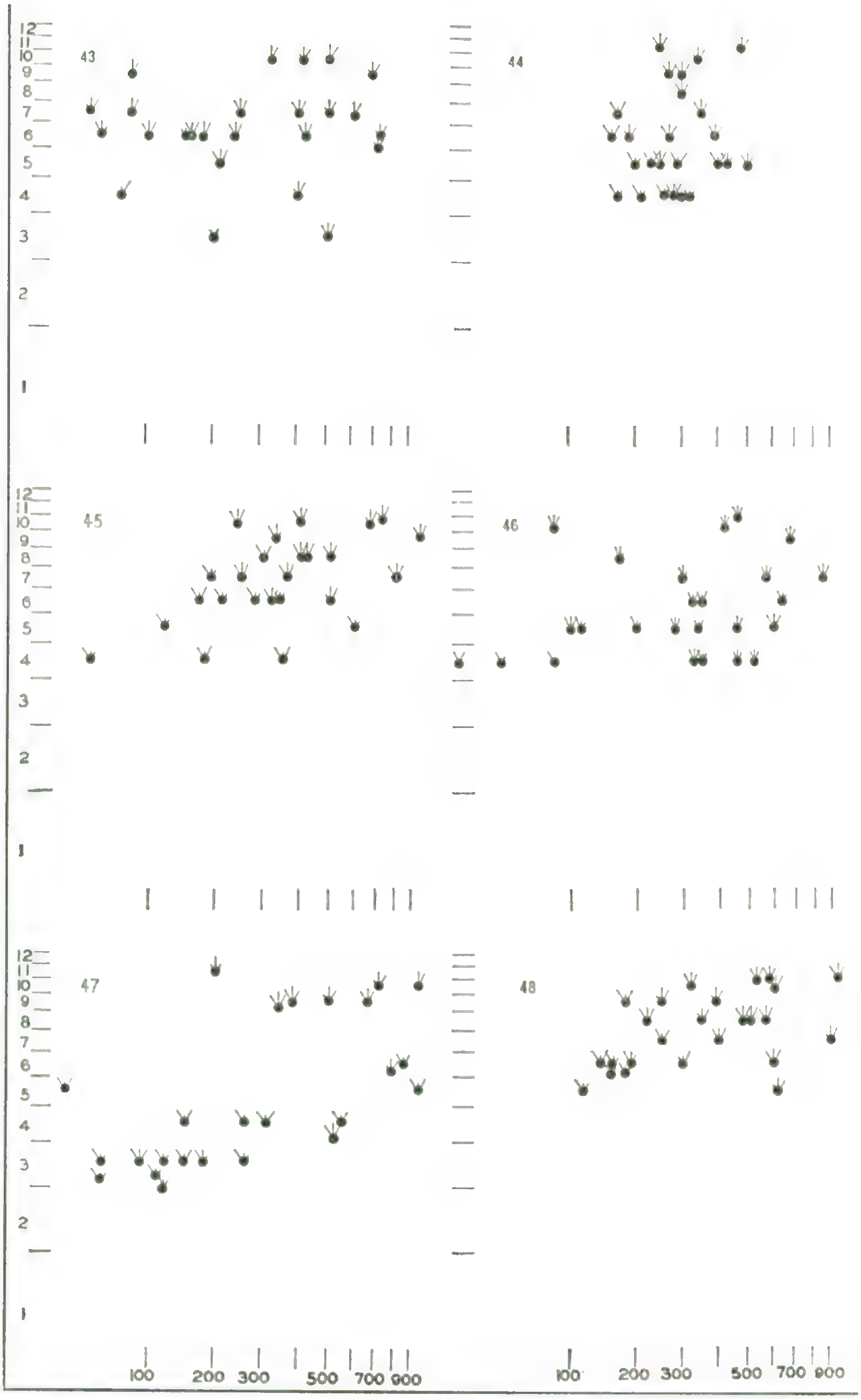
43
44
45
46
47
48
1
2
3
4
5
6
7
8
9
10
11
12
100
200 300
500 700 900
100
200 300
500 700 900

Fig. 16

to North Carolina and west to Nebraska and southern Texas. Some specimens outside this area were studied—southwestern New York state, southern Michigan, and the Atlantic Coastal region. Areas where *Juniperus virginiana* meets *Juniperus horizontalis* or *Juniperus communis* were not studied in detail.

Pictorialized scatter diagrams (Anderson, 1949) of each population were plotted on a log-log scale, but normal values for the characters were used. This technique was used chiefly to keep the populations on a single sheet. The log plots condense the high values and spread the low ones, effecting a diagram which displays the relative degree of variability very successfully.

In making up the scatter diagrams, all the six characters were used except that of leaf margin. The five characters were plotted, using different combinations of them for the abscissa and ordinate. In each case, even though the position of individual specimens varied somewhat, the total plot remained very nearly the same. However, it seemed most sensible to use either the characters with the greatest range or the greatest absolute difference; therefore, along the abscissa were plotted values for lateral whip and along the ordinate values for ratio of gland length to width. The data for the other three characters, per cent decussate foliage, length of whip leaf, and length of lateral whip, were grouped into three classes: (1) plants in which the measurements for each single character were *Ashei*-like, (2) *virginiana*-like, or (3), intermediate. *Ashei*-like characters had low values and were designated by a black dot; *virginiana*-like ones had high values and were designated by a dot with long rays; intermediate ones were designated by a dot with short rays. The legend on page 40 gives an explanation of the pictorialized scatter-diagram symbols.

Figure 18 is a pictorialized scatter diagram of a typical population of *Juniperus Ashei* (shown as squares) from the Edwards Plateau; of *J. virginiana* (shown as dots) from the Interior Low Plateaus; and of intermediates (shown as squares with superimposed dots) from Oklahoma and Missouri. This diagram is the heart

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Figs. 16–17. Locations represented by scatter diagrams 43–54, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2–3; "Pure" *J. virginiana*, 8–12. Explanation of symbols on page 40.

Fig. 16—

43.	Wichita Mountains, Cache, Comanche County, Oklahoma	Population mean 8.50
44.	Lebanon, Wilson County, Tennessee	8.56
45.	Fritchton, Knox County, Indiana	8.85
46.	Sumner County, Tennessee, near state line	8.96
47.	Harrisville, Arkansas	8.96
48.	Hadley, Warren County, Kentucky	9.00

Fig. 17—

49.	Eudora, DeSoto County, Mississippi	9.36
50.	Ninevah, Virginia	9.85
51.	Warm Springs, Virginia	10.80
52.	St. Louis, Missouri, Goetz Nursery. *J. virginiana* var. *Canaertii*	10.00
53.	Norman, Oklahoma, University Nursery. *J. virginiana* var. *Canaertii*	10.03
54.	Ann Arbor, Michigan, Ann Arbor Nursery. *J. virginiana* var. *Canaertii*	10.04

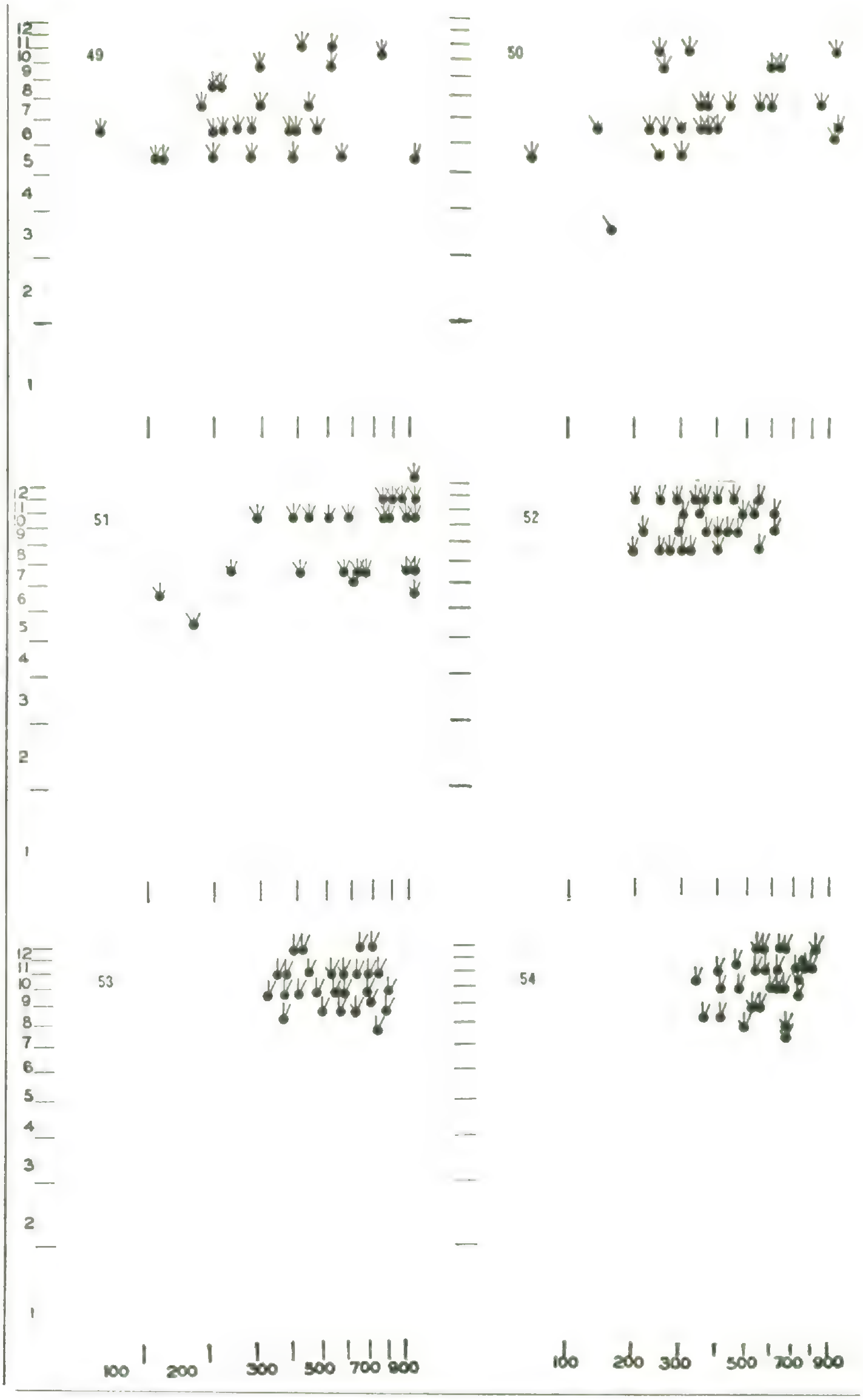


Fig. 17

of the study and demonstrates several important points: (1). The pattern of the recombinations is typical of interspecific crosses. The "recombination spindle" is fairly wide, suggesting that either the linkage is not exceptionally strong or else the natural plasticity of the characters is responsible for widening the "spindle." (2). No combinations occur which may be described as reciprocals. (3). The characters from each species tend to stay together in the intermediates, suggesting linkage. (4). More of the intermediates overlap or tend toward the characters of *Juniperus virginiana* than *J. Ashei,* which is probably the result of either differential introgression or differential selection of introgressants.

The data from the scatter diagrams were grouped to obtain a mean index value for each population. The coordinate positions were assigned values by means of a grid which divided the diagram into equivalent units from 0 (lower left of diagram) to 10 (upper right of diagram). The symbols were evaluated as follows: dot, 0; dot with short rays, 1; dot with long rays, 2. For any individual's index, its values were added to its coordinate position value. These were totaled for the whole population and divided by the number of individuals to obtain the mean index for the population. These grouped-data means corresponded closely to the population means obtained from the original measurements. This method was used because of the speed as well as the accuracy with which the populations could be typified. Obviously, these grouped data tend to obscure the differences within the populations of intermediates.

Map 2 uses the index values to indicate the character of the populations in their geographic setting. This map clearly indicates the geographic differentiation of *Juniperus virginiana* in relation to introgressive hybridization with *Juniperus Ashei.*

Geographic Races of *Juniperus virginiana*

Two races may be differentiated within the species *Juniperus virginiana* as a result of this study. They are here named *Typica* and *Ozark.*

Typica (area 1 on Map 3) is composed of two habitat forms which vary concordantly and have been known for some time by horticulturists as Eastern and Tennessee. Briefly, the Eastern form is the very tall, narrowly pyramidal tree which reaches its best development in the Appalachian Plateaus. Populations of the Eastern form have an index value from 9 to 10. This form is also found in the Central Lowlands as far west as the Shawnee Hills and throughout the Interior Low Plateaus. The Eastern form has an associated habitat form within part of its range with which it is morphologically concordant (Anderson, 1949). This more xeric form, known as Tennessee, is the slower-growing, smaller, straight-trunked, glade plant whose lowermost lateral branches are close to the ground even in old specimens. The Tennessee, which appears to be a diminutive of the Eastern, has index values from 7.5 to 9.0. This form is characteristic of the limestone glades (barrens) of the Interior Low Plateaus and may frequently be found growing near the eastern form but always in the most xeric habitats of the locale. The Tennessee form is best developed on the Lebanon limestone of the Nashville Basin.

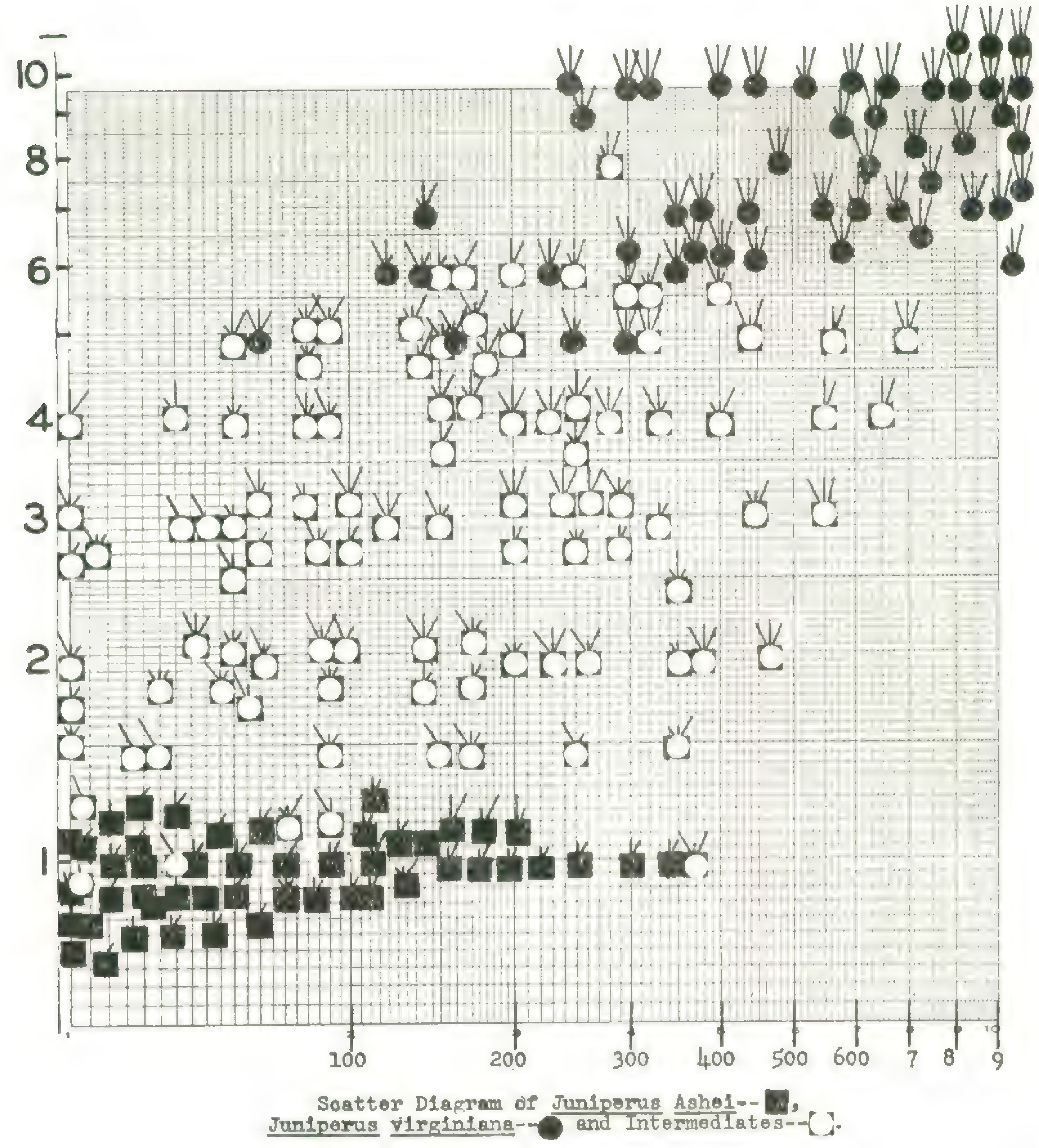
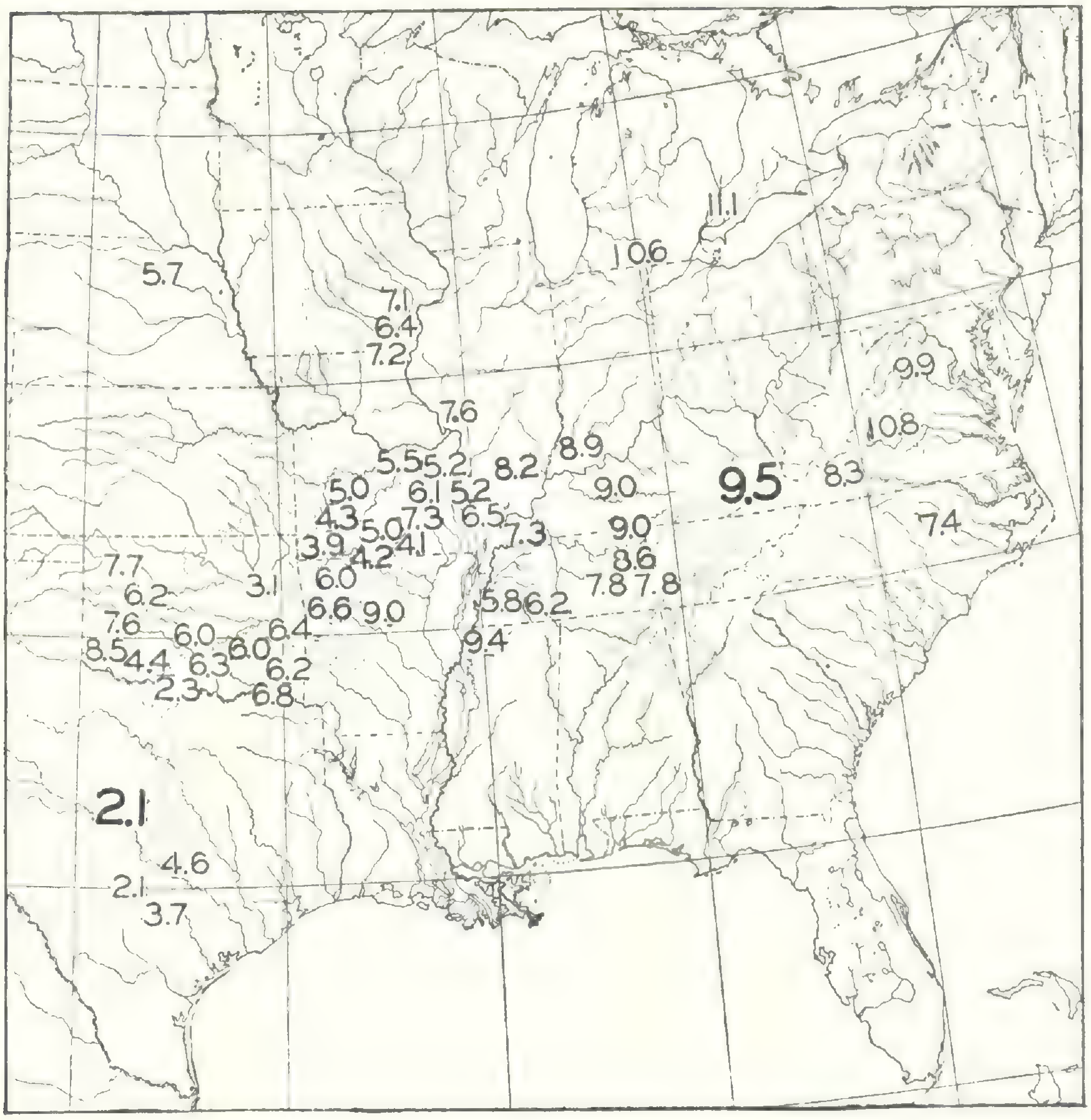


Fig. 18. Scatter diagram of *Juniperus Ashei*, *J. virginiana*, and intermediates represented by 200 individuals: 50 specimens of *J. Ashei* from the Edwards Plateau, 50 specimens of *J. virginiana* from the Interior Low Plateaus, and 100 intermediates from Oklahoma and Missouri. Gland length-width ratio is plotted on the ordinate; length of lateral whip on the abscissa. The bar values are the same as given for the diagrams (figs. 9–17) on page 40.

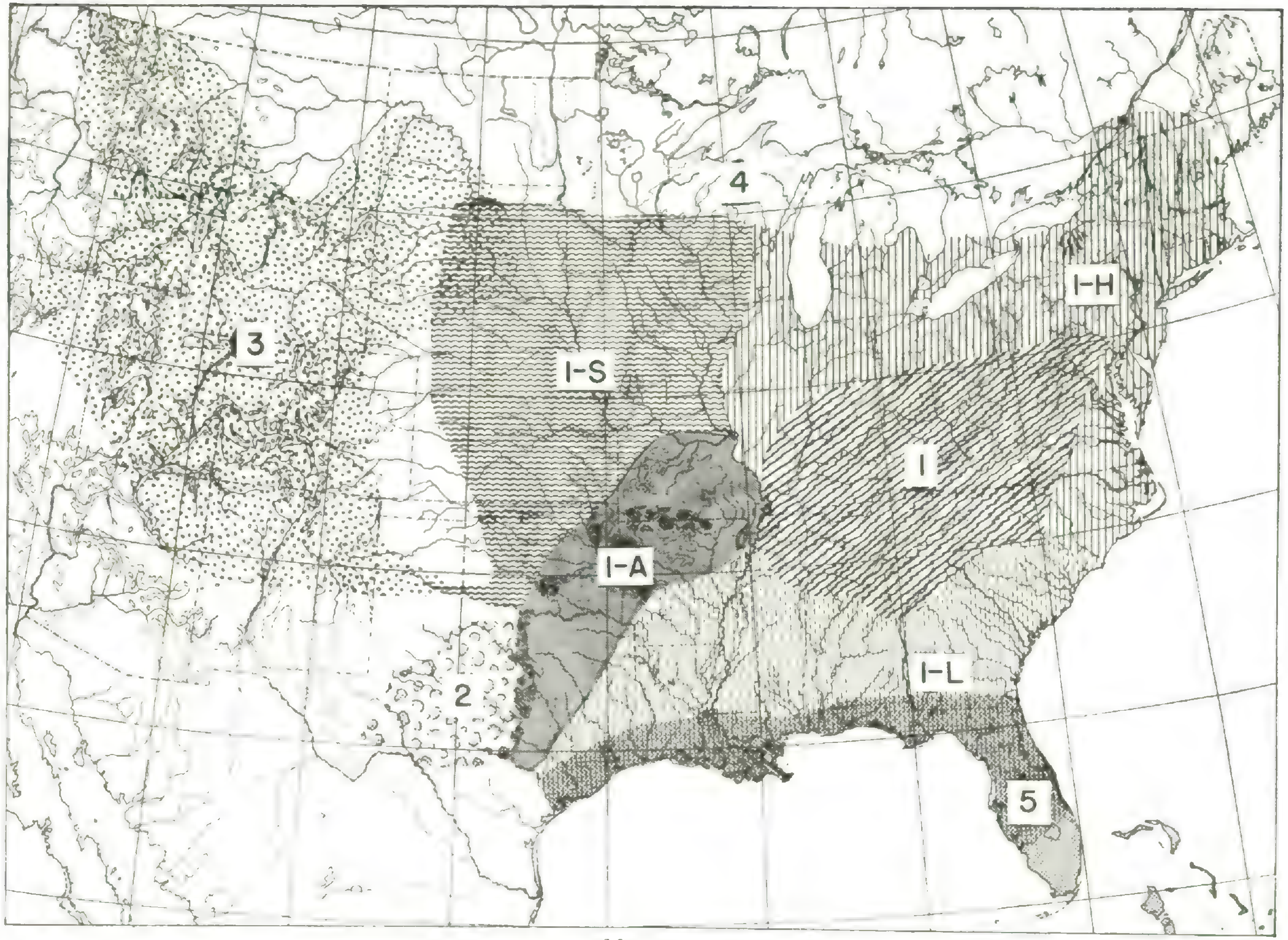
The Ozark race (area 1-A of Map 3) includes a most heterogeneous assemblage with index values ranging from 4 to 7. Populations which score approximately 4 are all hybrid swarms on limestone, usually dolomitic, knobs or glades made up of individuals with characters of either species. However, the index value of swarms may vary according to the ability of *Ashei* and *Ashei*-like individuals to survive in the habitat. The hybrid swarm at Platt National Park, Oklahoma, had an index of 6.3. The area is in the Oak-Hickory savannah (Bruner, 1931) but is open and covered with a dense stand of *Andropogon scoparius*. The soil originates from the



Map 2

The geographic distribution of population means for 54 populations (plotted to the nearest tenth).

calcareous Pontotoc Conglomerate. The water table is near the surface, so that this particular site, which is not well drained, is a somewhat unfavorable habitat for *Juniperus Ashei* and its putative relatives. The hybrid swarms of the bald knobs in southwestern Missouri are in much more xeric environments—dry limestone knobs with thin rocky soil formed by erosion of the Burlington limestone. This limestone occurs in flat layers (giving the effect of laminated terraces) which are relatively impervious and, except where the slope is steep, do not drain too well. Likewise, ground water does not readily find its way back into the soil above the layered rock. Thus, these areas are wet in early spring but very dry in summer and fall. The tops of the knobs and the southwest slopes are favorable habitats for *Juniperus Ashei,* while the rest of the area is thickly populated with the introgressants; hence the low per cent of *Ashei* at Platt and the high per cent on the knobs. Populations which score 5 are situated on bluffs or glades. Those with



Map 3

Distribution of species: Area 1 (and 1-A, 1-B (1-L on map), 1-H, 1-S), *Juniperus virginiana;* Area 2, *J. Ashei;* Area 3, *J. scopulorum;* Area 4, *J. horizontalis;* Area 5, *J. barbadensis.*

Distribution of introgressants of *J. virginiana:* Area 1-A, Ozark race *(J. Ashei)*; Area 1-B (1-L), Florida race *(J. barbadensis)*; Area 1-H, Northern race *(J. horizontalis)*; Area 1-S, Platte River race *(J. scopulorum)*.

score 6 are similar to *Typica*, and in the Ozarks they grow in open woods, prairies, and along creeks and rivers. They are much more heterogeneous (discordantly varying) than *Typica.*

The evidence indicates that the Ozark race with all its heterogeneous forms is a product of the mixing of the southwestern species, at times past and to some extent at present, with the eastern species and the subsequent selection of gene combinations distributed by birds, water, mammals, and man. The strength of the evidence is morphological and lies in the presence of combinations of characters of the two species of the Ozark Highland and the Southwest. These combinations of characters mostly have their replicas in the hybrid swarms and from them spread many miles and along many lines of selection.

Discussion

The problem presented in this paper is merely one portion of the problem of variability in *Juniperus virginiana.* It deals with the effect of hybridization and introgression between *Juniperus Ashei* and *J. virginiana.* Each species is influenced by other species not included in this study: *J. Ashei* where it meets *J. Pinchotii* and *J. monosperma;* and *J. virginiana* where it meets *J. horizontalis, J. scopulorum*, and others.

The index map (Map 2) shows the apparent extent of influence of *Juniperus Ashei* on *J. virginiana.* This influence is measurable only in the Ozark Highland and southwestward, and in the South perhaps as far as the Tennessee River. Populations of *J. virginiana* with means from 4 to 7, whether mixed or not with actual specimens of *J. Ashei*, still show influence of the germ-plasm of the southwestern species. The criteria are morphological and based on combinations of characters from each species.

The population mean does not give a very good picture of the individuals which make it up (compare the scatter diagrams for populations 23, 24, 25). For example, in the Caddo Canyon (23) population the influence of *Juniperus Ashei* is only slight as compared to that in the Platt National Park (24). The same holds for the Poteau population (25). In the Platt National Park there are greater and more frequent extremes, but the mean is practically the same. Yet, the more homogeneous populations still show characters of each species. The most conspicuous differences among the three populations are in the habitats.

The canyon rim population from Caddo Canyon is in the tall-grass prairie above the deep canyons of Sugar Maple forest. The canyon vegetation is classed as a post-climax deciduous forest relic (Little, 1939). There is abundant massive red sandstone (Whitehorse formation) which has permitted the Washita and South Canadian Rivers to cut deep canyons into the ridge separating their flood-plains. Cedar-brakes and tongues of short Post Oak-Black Jack Oak savannah frequently follow the creeks into the tall-grass prairie. The annual rainfall is approximately

30 inches. Junipers on the rim show obvious affinities to *Juniperus Ashei:* some are bushy; others have very long up-turned basal branches; still others have slightly toothed leaves which under a compound microscope show the characteristic hooked cells. They have larger fruit than does typical *J. virginiana,* but there are no real extremes in either direction. The area is not suitable for the calciphilous southwestern species and its extreme recombinations. There are present only the less dramatic intermediates. On the canyon floor, 100 feet below, *J. virginiana* is entirely different and shows obvious affinities to *Juniperus scopulorum,* not *J. Ashei.*

The Poteau, Oklahoma, population is growing on the resistant sandstone bluffs and banks of the Poteau River which flows in the Arkansas Valley Province in the Oak-Hickory savannah vegetation zone. Even though the average annual rainfall is 44 inches, the coarse porous sandstone and steep banks of the river insure rapid drainage, and the open savannah country permits high transpiration. Since the area is not suitable for the extremes of *Juniperus Ashei,* it is not surprising to find intermediates, not of a striking nature, but homogeneous enough to give a mean corresponding to that of the hybrid swarm of Platt National Park.

It is most important to realize that the habitats of *Juniperus* can be roughly defined more efficiently by a mass collection than by the various paraphernalia for measuring physical factors of the environment. This is possible only after one has gained knowledge of and experience with the organisms in question. This generalization holds only for introgressing species which have distinctive ecological differences. The heightened variability is made possible through extensive long-term hybridization, possibly discontinuous in time, from which various environments along the way have selected those plants able to establish and reproduce themselves. This is a dynamic process and demonstrates that just as individuals and species are constantly changing, often in multi-faceted ways, so also are the colony, the community, and the association; thus, here is the accentuation of Cooper's (1926) classic expression, that so-called climax formations are only "variables approaching a variable," a continuum.

Population studies are valuable to the ecologist, since they shed light on the relations of the taxons, the environment, and natural selection. It is a problem of "workman know your tools." The ecological potentials of the partially discontinuous genotypes making up the species complex or complexes, even though not precisely known, are predictable on a considerably better basis than guesswork. Such complex populations with no absolute internal discontinuities are bound to have almost inexplicably complex ecological patterns. Such species have great survival value in the face of changing environments.

Ecotypic differentiation must be greatly accelerated following introgression, especially if the ecological requirements of the introgressants are relatively different. It is quite likely that mixing of germ-plasm is responsible for the wide range of distribution of *Juniperus virginiana.* Reference to Map 3 will show the

feasibility of such an hypothesis. The central area indicated on Map 1 is the only area where homogeneous Red Cedar exists. The other areas support heterogeneous Red Cedar tending in the direction of an adjacent species. In fact, we owe to this phenomenon of introgression a great many new horticultural varieties of both Red Cedar and Rocky Mountain Juniper. The Platte River type is not pure *J. virginiana* but mixed with *J. scopulorum*. Many of the varieties selected from the Black Hills and other areas by Mr. D. Hill are introgressants. Introgression is an intensifier of variation and seemingly a potent force in speciation.

The question now arises, when and of what duration did the hybridizing occur between Ashe Juniper and Red Cedar? It is inconceivable that it was of recent occurrence, because of the high degree of differentiation in populations and because of the distance from present-day naturally occurring *Juniperus Ashei*. However, it is known that present-day Ashe Juniper occurs along the early-day cattle trails over which Texas herds were transported overland to St. Louis (Parker, 1854). Wolff (1948) states a case of a small juniper plantation developing in the treeless part of Kansas as a result of a cattle drive from Texas. It is possible that even in earlier times buffalo might have dispersed numerous seeds. Likewise, small mammals or birds might have helped these seeds to find a cliff site and become established, sheltered from the alleged frequent fires set by the Indian and white man. From this vantage point, pollen could easily be rained onto the Red Cedar along the creeks, rivers and lesser bluffs. Since promiscuous firing ceased in recent years, the species moved out of the bluffs onto knobs, glades, and ridges, and the introgressant recombinations began to spread to every possible habitat. This, of course, implies a rather terrific rate of migration and ecesis. Even so, these possibilities do not express adequately in terms of time and space the probable generations of backcrossing required to get so complete a spread of the characters of the two species throughout the Ozarks. This hypothesis does not explain the fact that the knobs and glades also represent a whole community of southwestern plants as described in the section on "Ecology."

The most probable interpretation is that mixing in these two species has occurred some time or many times in the past as a result of the climatic fluctuations and consequent floral migrations during and following glacial epochs. The presence of hybrid swarms in restricted areas today is merely a remnant of, or a clue to, the far more extensive migrations and mixings in the past. This hypothesis sheds light on the existence of marked ecotypic differentiation of Red Cedar in the Ozark Highlands, Oklahoma, and Texas. Even today, those fluctuations of climate, which are reflected in the epicycles of erosion in the Southwest (Bryan, 1929, 1940, 1941), probably aid in maintaining the southwestern elements (the present cycle being favorable) on the glades and knobs of the Ozark country, in the absence of repeated burnings. When and if such fluctuations become more severe and consequently more general, they may be sufficient to enlarge the areas in which rates of change characteristic of the Southwest occur.

This may well lead to a marked upset in the balance of things. Such was the case in Pleistocene time.

The historical events discussed above have probably not contributed directly to the structure of the present-day populations of *Juniperus* in periglacial areas. Historical factors, in the geologic sense, probably affect the stabilization of only the most fundamental characters of plant groups, for example, xeromorphism, heliophytism, hydrophytism, and mesophytism. To consider a single historical event, such as isolation in past ages, as the factor responsible for the structure of a modern population or species complex, lumps a great many important processes and events, perhaps more current ones, as impotent forces. It seems more appropriate to consider every force which affects an organism, whether in the Tertiary or yesterday, as an historical factor.

Where introgression is involved, the significance of the historical factor lies in the degree of juggling of germ-plasms made possible through fluctuations in distribution which cause allopatric species to meet. The resultant hybridization enriches the field of variability within the species involved. However, the part of that variability which is subsequently preserved and distributed has little to do with an historical factor in the geologic sense but is determined by the presence and continuity of suitable current habitats.

The final aspect of this work revolves about the question—What is *Juniperus virginiana?* It is, as any field botanist knows, a very complex species which has a distribution befitting a weed. The species has never been fully analyzed and is not likely to be except on a long-term basis. Map 3 illustrates the pattern of differentiation in *J. virginiana* and its geographic relations with other species.

Fassett's (1944, 1945) studies have shown introgression to occur between *Juniperus virginiana* and *J. horizontalis* in the northern states. The pattern of differentiation suggests that hybridization has occurred over a long period of time, since these two species have probably been continuously contiguous since late-glacial time. As a result of Fassett's work and my own field observations, I tentatively set aside area 1-H on Map 3 as the *Northern* geographic race of *Juniperus virginiana.* It is differentiated from *Typica* by having slightly larger fruit, wider and longer whip leaves (12 to 17 mm. long by 1 to 2 mm. wide), longer whip leaf glands (5 to 10 mm.), generally more elliptic, wider spur-leaf glands, a high percentage of curved peduncles, and a high frequency of quadrangular microsporangiate cones. All these characters are in the direction of those of *Juniperus horizontalis.* The habit ranges from var. *crebra* to the typical pyramidal form to var. *ambigens.* On the Coastal Plain of the Atlantic, grotesque forms similar to var. *ambigens* are found, with most of the leafy branches on the offshore sides of the plants. They have coarse whip shoots and long whip leaves with a high frequency of double glands.

The Appalachian Plateaus and the Interior Low Plateaus are the home of the purest Red Cedar, *Typica,* in terms of the amount and extremes of variation and

of the degree to which the populations are free from morphological resemblance to adjacent species. *Typica* and *Ozark* (area 1 and 1-A, respectively, on Map 3) are discussed on previous pages.

On the Gulf Coastal Plain, there is a loose, lax, almost weeping, small-fruited *Florida* race (area 1-B [1-L] on Map 3) which blends into *Juniperus barbadensis.* The relations of this Coastal Plain material, including what is called *J. barbadensis,* to the species of *Juniperus* on the islands in the Caribbean is not at all clear. In the western part of the Coastal Plain as far east as Fort Bulow, Louisiana, there are a few hybrid specimens between *Juniperus virginiana* and *J. Ashei.*

From Fassett's studies of populations from Nebraska northwestward and my studies in western Oklahoma and Texas (Palo Duro Canyon), I designate another geographical race, *Platte River* (area 1-S on Map 3), which may be differentiated from *Typica* by having a high frequency of spur leaf glands close to the leaf tips, a high frequency of non-overlapping spur-leaf tips, slightly larger fruit than *Typica,* long secondary branches with short tertiaries giving a wand-like aspect, acute angle of ascent of the secondary branches giving the aspect of "reaching for the stars." This generally very beautiful race shows modified characters of *Juniperus scopulorum.* These junipers from the Wichita Mountain Wildlife Refuge of southwestern Oklahoma, or the Palo Duro Canyon, Texas panhandle, or the Platte River bluffs of Nebraska, should be prized as seed stock and propagating stock for the high-plains country.

These geographic races are not clearly defined in the sense that each is homogeneous. The species *Juniperus virginiana* is apparently quite youthful, and as a result of introgression from other species it is in the process of becoming polytypic. The fact that junipers are favored in disturbed areas, together with their facility of distribution, inhibits the stabilization of the heterogeneous races. Whether or not these discontinuities ever become absolute is a matter for conjecture.

It seems evident that introgression is probably not a cataclysmic force in evolution but nature's subtle way to bring the elements of the landscape back into some sort of balance during and after change. If climatic change is such that a species migrates and meets a close relative, the habitat at the meeting place may not be very suitable for either species; but through hybridization nature makes new organisms which are actually a product of the change, and some of them will likely be well adapted to the new conditions. Such a process may have widespread effects, but that depends on the distribution of suitable habitats and the efficiency of dispersal of the particular species.

Certainly, introgression is playing a major role in the evolution of *Juniperus virginiana* as an incipient polytypic species. The regions of differentiation shown on Map 3 are rather clearly defined. Because of the tremendous quantities of pollen and seeds produced and the ease with which they are transported over long distances, these population types tend to be swamped by recombining characters; thus the characters do not become stabilized readily, and the boundaries of the elements tend to fluctuate considerably.

Summary

Knowledge of the existence of hybrid swarms between *Juniperus Ashei* and *J. virginiana* led the author to make population studies with the hope of demonstrating the nature and extent of the influence of the two species upon one another. The evidence for hybridization is the character recombinations of the two species in many specimens found where these species grow together.

The comparative morphology of typical members of each species was intensively studied. From the information obtained characters best contrasting the two were selected and used in scoring populations from Virginia and Michigan to Texas. These characters were: ratio of gland length to width, length of typical terminal whip leaf, length of terminal whip at the apex of a typical secondary shoot, length of lateral whip on the same secondary shoot, and percent of decussate spur shoots on the secondary shoot.

These data were converted to pictorialized scatter diagrams so as to integrate the simultaneous variation of several characters. Also, an index was made based on these same characters. A value of 2 was typical for *Juniperus Ashei*, a value of 9.5 for *J. virginiana*. Hybrid swarm mean index values ranged from 3.9 to 6.3, depending on the characteristics of the particular environment and the relative numbers of the two species present.

The index values were plotted on a map to show the geographic distribution of population characters. The results indicate that *Juniperus Ashei* influences *J. virginiana* by introgression throughout the Ozark Plateau and probably as far east as the Tennessee River in the vicinity of the 36th parallel. The reciprocal influence is quite clear but not as common or as extreme. This is undoubtedly because *Juniperus Ashei* has invaded far into the range of *J. virginiana*, while the reciprocal action has not occurred to as great an extent.

A number of hybrid swarms from Missouri to Texas were studied in detail. Glade and bluff junipers in the Ozarks have replicas in those hybrid swarms. This is not true of the glade and bluff junipers of the Interior Low Plateaus.

It is postulated that this introgressive influence was initiated by the fluctuation of the ranges of the two species consequent to climate fluctuation during and following the glacial epochs. Thus, opportunity was afforded these two highly distinctive but sexually compatible species for free hybridization and, especially, for consequent selection of favored back-crosses. The extreme heterogeneity of the junipers of the Ozark Plateau may be explained by this hypothesis. This is obviously a means by which the field of variability of a species may be increased with subsequent changes in ecotypic differentiation through differential selection.

The differentiation of *Juniperus virginiana* as a species is discussed. It embraces five races: (1) *Typica* (the pure species), (2) the *Ozark* (introgressants with *J. Ashei*), (3) the *Platte River* (introgressants with *J. scopulorum*), (4) the *Northern* (introgressants with *J. horizontalis*), and (5) the *Floridan* (introgressants with *J. barbadensis*).

It is postulated that the genus *Juniperus* has evolved along the line of xerophytism, and that *J. virginiana* and *J. barbadensis* have secondarily been selected in the direction of mesophytism. The apparently youthful species *J. virginiana* is in the process of becoming polytypic as a result of introgressive hybridization with four other species. This process is retarded because of the swamping effect of character recombinations as a result of the high efficiency of pollen and seed dispersal and the great numbers of progeny produced. There is little chance for populations to become completely isolated even over great distances.

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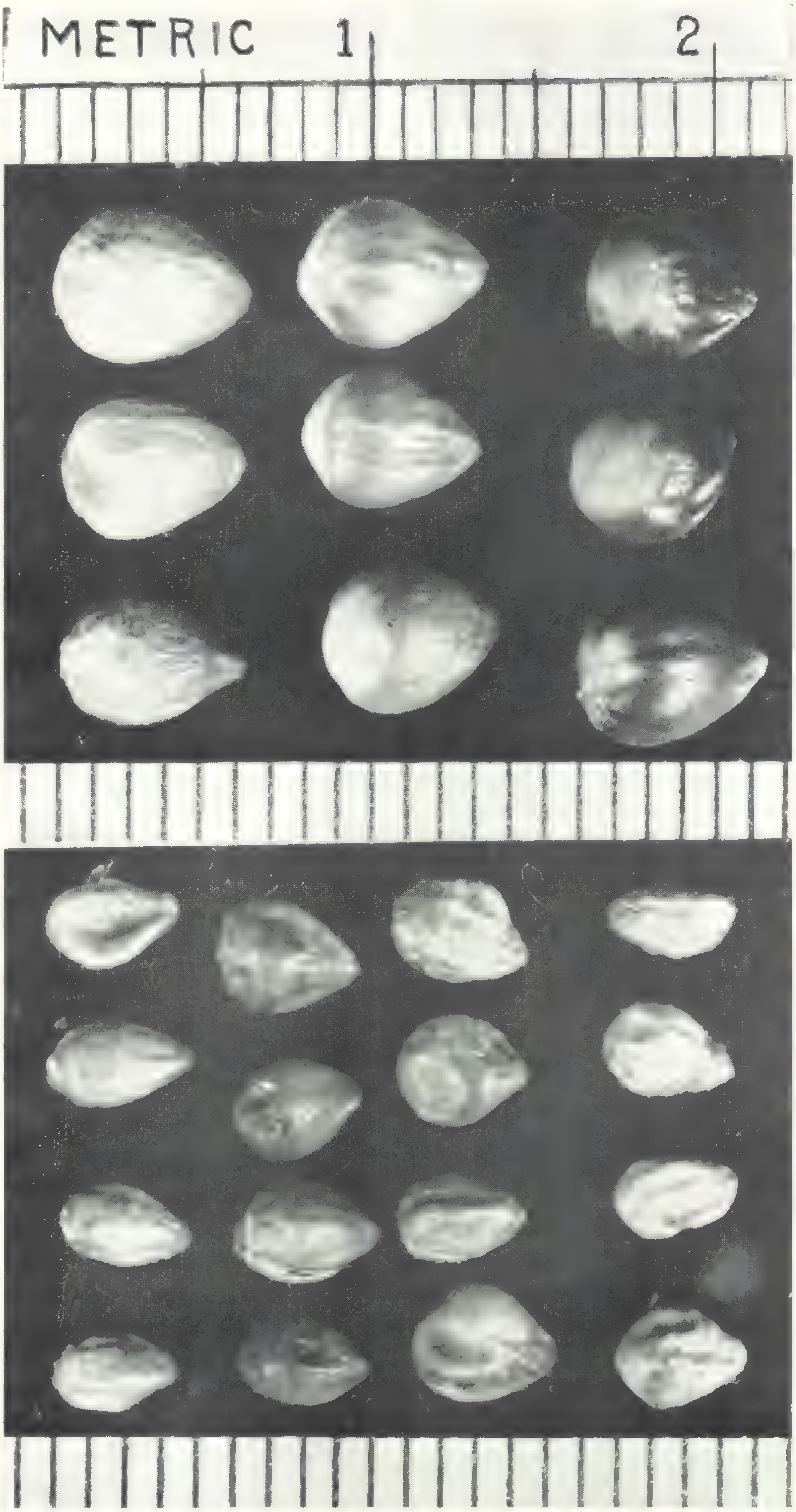
Explanation of Plate 1

Fig. 1. Seeds of *Juniperus Ashei:* top row, typical plants of the Edwards Plateau; middle and bottom row, from hybrid swarm near Austin, Texas. Scale is in millimeters.

Fig. 2. Seeds of *Juniperus virginiana:* top row, typical plants from Virginia; remaining rows, from hybrid swarm near Austin, Texas.



1

2

HALL—VARIATION IN JUNIPERUS

SPIKELET VARIATION IN *ZEA MAYS* L.*

REINO OLAVI ALAVA**

Introduction

In classifying the different varieties of Indian corn, *Zea Mays,* scientists have paid little attention to comparative floral morphology. Since the kernel is economically the most important part of the maize plant nearly all classifications have been based on its texture and morphology. The most recent classification is that of Sturtevant (1899), which is based on the characteristics of kernel texture and the development of husks around individual kernels. We may summarize Sturtevant's classification as follows:

Zea tunicata, the pod corns: "each kernel is inclosed in a pod or husks."

Zea everta, the pop corns: "characterized by the excessive proportion of the corneous endosperm and the small size of the kernels and ear."

Zea indurata, the flint corns: "readily recognized by the occurrence of a starchy endosperm inclosed in a corneous endosperm."

Zea indentata, the dent corns: "recognized by the presence of corneous endosperm at the sides of the kernel, the starchy endosperm extending to the summit."

Zea amylacea, the soft corns (the flour corns): "recognized by the absence of corneous endosperm."

Zea saccharata, the sweet corns: "a well-defined species group characterized by the translucent, horny appearance of the kernels and their more or less crinkled, wrinkled, or shriveled condition."

As Anderson and Cutler (1942) have pointed out, this classification is an artificial one and is of aid only in cataloguing different varieties. It does not indicate relationships between different groups or varieties.

Details of floral morphology are among the most important characters in the taxonomy of grasses. Although all the maize varieties, as far as we know, belong to one botanical species, investigations made thus far have shown that comparative morphological studies of reproductive organs can be of great importance. During their long existence many of the varieties of maize have become fairly constant. In some cases the morphological differences between different strains of maize are like those between closely related species of wild grasses.

Not only does the study of the spikelets of the tassel give us a new character for understanding the natural classification of the present-day varieties of maize, but it may also give important clues to the origin of these varieties. During the

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. This study was carried out as part of a special fellowship sponsored by the Pioneer Hi-Bred Corn Company, Johnston, Iowa.

**Botany Department, University of Turku, Finland.

last decades archeological discoveries in several different localities in North and South America have yielded interesting prehistoric and pre-Columbian material. The great majority of these maize remains which have found their way into museums are ears, shelled cobs, and loose kernels. Fewer tassels have been excavated and catalogued but still there is a fair number of tassels and tassel fragments, enough at least to give a clear picture of the characteristics of that part of the plant. The best of these remains are extremely well preserved although hundreds, or even thousands, of years old, and they can accurately be compared with material obtained from present-day varieties. By comparing archeological maize remains with each other, one can determine variation in prehistoric times. By comparing modern varieties with archeological material it is possible to show in which characters and to what extent changes have taken place. Until we have learned to know the ancient varieties, we shall not be able to understand the differences in modern varieties. Knowing now some of the primitive types of maize we are able to tell something more about the migrations of Indian corn from one area to another, perhaps even from one continent to another.

Both male and female flowers and inflorescences deserve study. There are, however, many external and mechanical factors which cause complicated differences in female spikelets, such as the pressure of the husk leaves, the pressure between kernels in the ear, the development of bony tissues, etc. Male spikelets, on the contrary, develop free in the open tassels and are much easier to handle and prepare than female ones, which are always partly hard and bony, partly thin and membranaceous.

For practical corn breeding the knowledge of both tassel and male spikelet characters is a valuable tool. Since the tassels reach maturity early in the growing season, the corn breeder can tell something about the offspring by knowing the male spikelet character, long before the kernels and ear show any of their mature characteristics. The present paper is a beginning at analyzing the variation of the male spikelets of maize. It is an attempt to determine in which characteristics variation takes place and how it can best be measured.

Previous Morphological Studies

REVIEW OF LITERATURE

The first morphological studies of *Zea Mays* were concentrated almost entirely on the origin and the structure of the female inflorescence. In them students were trying to understand the complicated structure of the ear of maize. So much did this structure intrigue them that virtually no studies of the male inflorescence were made until the twentieth century.

In recent decades, in analyzing the male inflorescence, several workers have noted rather marked morphological correlation between it and the female inflorescence. The type of correlation is usually referred to as the "homology of the ear and tassel." The earliest discussion of this idea is found in a paper by Mrs. W. A.

Kellerman (1895). It was her opinion that primitive maize had been a plant branching from many nodes, each branch with a terminal inflorescence similar to the maize tassel of the present day, but with bisexual flowers. Through selection the male flowers became more numerous in the terminal inflorescence of the main stem, while the female flowers became more numerous in the inflorescences of the lateral branches. Being in a more favorable position as regards nutrition, the central axis of the inflorescences in the lateral branches developed more strongly, while the branches of these inflorescences became reduced; as Kellerman puts it:

> The central stem of the "tassel" borne by the primitive branch by virtue of its more favorable position drew into itself the main force of the branch and became more highly developed at the expense of the surrounding tassel branchlets, the latter being finally entirely aborted. (Kellerman, 1895, p. 44).

Kellerman's statement, although not based on any reported detailed studies, made later students of the maize plant pay more attention to the question of the homology of the maize ear and tassel.

In attempting to explain the difference in the structures of the central spike and of the rest of the tassel, Collins came to the conclusion that:

> If one assumes a profusely branched panicle in which the branches have been reduced until each branch is represented by a single pair of spikelets, the inflorescence becomes a spike. If such a reduction of branches is confined to the upper part of the inflorescence, a type is produced resembling that of maize. (Collins, 1912, p. 526).

A more detailed study of the structure and phylogeny of the maize tassel was first made by Weatherwax (1935). He studied a number of inflorescences of different species of grasses, both related and unrelated to maize, and came to the conclusion that the present-day maize tassel, a compound inflorescence of a number of raceme-like branches having their spikelets in pairs, may be a result of several steps in evolution. It may have developed from a primitive type of inflorescence, a panicle with loose branches, the spikelets not arranged in pairs. The raceme-like structure of the branches of the maize tassel and the arrangement of the spikelets in pairs may have had an independent evolution since grasses of several genera, not closely related to each other or to maize, have one or the other of these characters in their inflorescences or, as in maize, both.

The development of both the male and female inflorescences of maize was first studied by Bonnett (1940). He discovered that from the germination of the kernel to the dehiscence of the anthers the plant passes through two stages. In the first, only vegetative parts, leaves and axillary shoots, are produced, while the differentiation and development of the inflorescences take place in the second stage. In the tassel the secondary branches develop first, and from their bases the tertiary branches later start their development.

As mentioned previously, the classification of maize varieties made by Sturtevant (1899) was an artificial one. Anderson and Cutler (1942), realizing the need for a more natural classification, studied the external morphological characters of maize which would be useful criteria for the descriptions of strains and varieties.

The number of tassel branches was found to be surprisingly stable for a variety and to be one of the most useful characteristics. The stiffness of the tassel branches, the length of the sterile zone at the base of the secondary branches, the degree of variation in the spikelet and the arrangement of the spikelets, and the presence and degree of condensation were found to be some of the best characters for distinguishing different varieties. By "condensation" is understood the situation in the secondary branches, where the internodes are so telescoped together that several spikelet pairs appear whorled at one node instead of being alternate at several nodes.

Although the homology of the ear and tassel had been suggested by several earlier authors it had not been investigated in detail until the studies of Anderson (1944b). Around 1940 he began to study the morphological correlation between the male and female inflorescences, realizing that a thorough knowledge of the maize tassel is not only important as such but is also the best key for understanding the phenomena of the ear. The characteristics which are so closely correlated with each other in these two inflorescences are much more readily studied in the tassel. While working with many different varieties of maize, Anderson studied the cause of row numbers above 8 and 10 and found row number to be correlated with condensation, a correlation particularly close in North American varieties. After more detailed studies, Anderson and Brown (1948) came to the same conclusion.

Another important fact found by Anderson (1944b) is the close correspondence between the relative and absolute lengths of the secondary tassel branches, on the one hand, and the shape and size of the ear, on the other. The presence of tertiary branches was found to be correlated with the irregular arrangement of the kernels at the base of the ear—a character relatively common in certain varieties of maize.

While condensation is rather common in some North American races of maize it is much less so in South America. There multiplication, a phenomenon which also increases the number of kernels on the ear, is more common than it is in North America. Multiplication has been described by Cutler (1946, p. 269) as producing tassels "with the sessile and pedicellate spikelets alternating at the nodes as if the primordia had branched to give rise to more pairs of spikelets."

Studies on the homology of the ear and tassel of maize, as well as on the morphology of different tassel characters, have given a clearer picture of the phenomena in both of the inflorescences. Bonnett (1948) found that at the early stages the tassel and ear are morphologically scarcely distinguishable from each other. At a certain stage of development the ear becomes progressively thicker and harder and the tassel progressively more lax and expanded. According to Kiesselbach (1949), the differentiation of the ear and tassel begins very early, and three weeks after planting, the entire stem, surmounted by the differentiated tassel, may have been formed.

Just as the earlier students of maize concentrated their attention upon the female inflorescence, the ear, so in studying the spikelet did they devote themselves

almost completely to the pistillate flowers. In Malpighi's 'Anatome Plantarum' of 1675 (Arber, 1934, p. 362) appears what is perhaps the first illustration of the staminate spikelet of maize, an illustration which clearly shows the different parts of the spikelet. Despite this early example of careful attention to the details of the staminate spikelet nearly two and a half centuries elapsed before further progress was made.

Weatherwax, in his study of anomalous flowers in maize (1925), mentions that the primordia of the two spikelets appear at an early stage of development, and that the upper primordium, which later becomes a pedicellate spikelet, is regularly the more advanced. Bonnett (1948) discovered that at the beginning of spikelet formation the branch initials, which already are unequal, divide into two parts. The larger becomes the pedicellate spikelet and the smaller the sessile one. In the staminate spikelet flowering parts differentiate in this order: first, the empty glumes, then the flowering glumes, and finally the anthers, the differentiation and development of the anthers being the main growth activities. The pistil may start to develop, but usually it remains rudimentary. Kiesselbach (1949) found that the flower formed at the original growing point of the spikelet is the terminal one; the lower flower is developed from the growing point which is somewhat later formed at the axil of the lower glume. Cutler and Cutler (1948) have studied the morphology of both staminate and pistillate spikelets and florets of maize, and compared it with that of related grasses in the tribes Maydeae and Andropogoneae. They found that the normal staminate spikelet of maize consists of two sterile glumes, the outer and inner ones (or the lower and upper ones) enclosing two flowers, and that the flowers consist of the flowering glumes, a lemma and a palea, two lodicules, and three stamens.

As several students of maize have pointed out, there are significant differences in the spikelets which are characteristic for each variety or group of closely related varieties. One of these characters is the morphology of the lower glume, which, combined with other characters, is useful for the recognition and description of maize varieties and races, as pointed out by Anderson and Cutler (1942).

Material and Methods

The material used in this study is mostly from Dr. Edgar Anderson's large collection of maize specimens from different parts of the world. Much of it was collected from cultivated fields, while a part was grown outside its original range in experimental plots. The Northern Flint varieties are partly from the Pioneer Hi-Bred Corn Company's herbarium at Johnston, Iowa. Five varieties of Bolivian corn are from Dr. Hugh Cutler's collection at the Chicago Natural History Museum. The prehistoric material from Arica, Chile, has been placed at my disposal by Mr. Junius Bird of the American Museum of Natural History, and that from Bat Cave, New Mexico, by Dr. Paul C. Mangelsdorf of the Botanical Museum of Harvard University. The author is indebted to all these individuals and organizations for the tassel specimens which they so kindly supplied and without which this study would have been impossible.

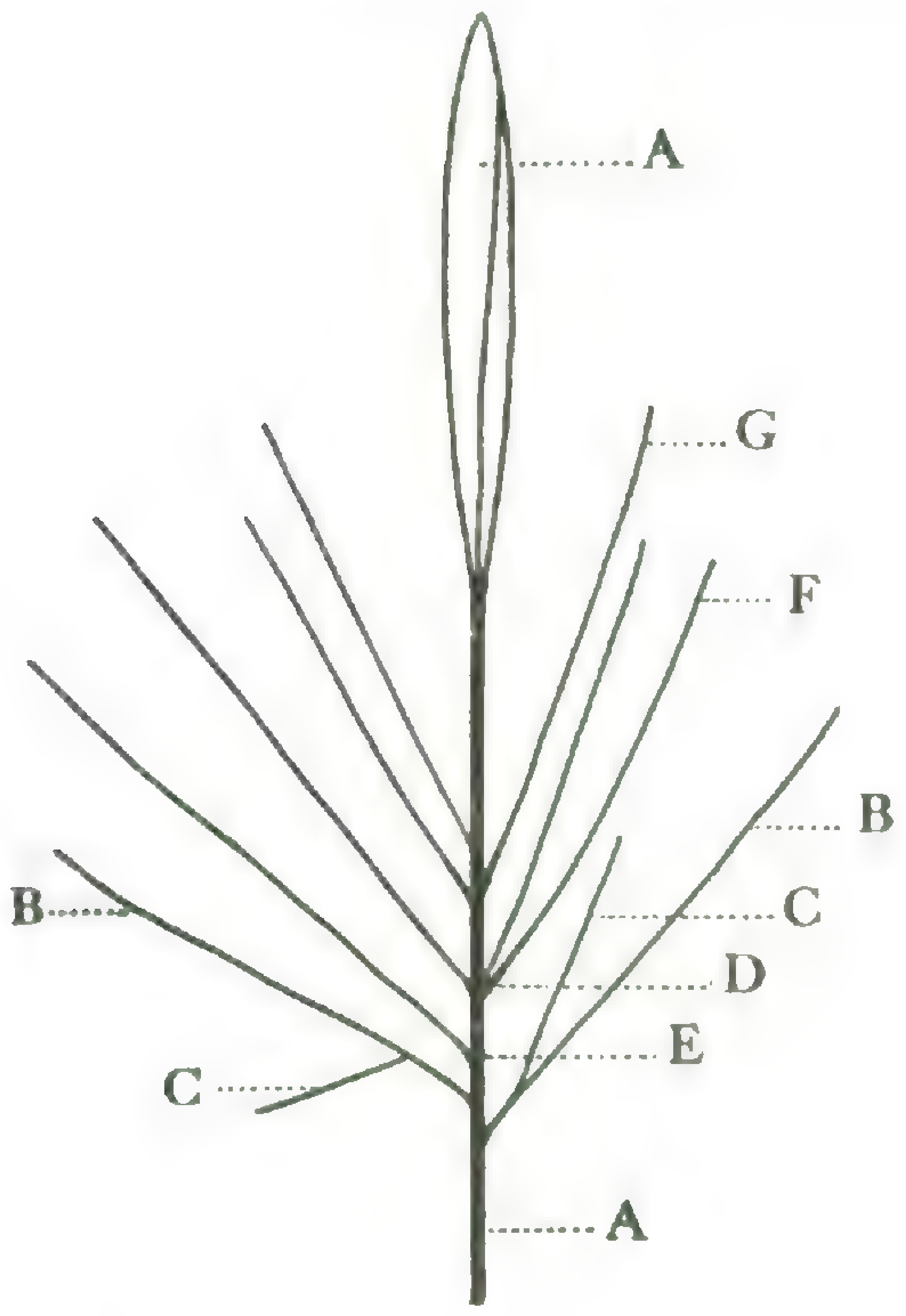


Fig. 1. Diagrammatic drawing of an average maize tassel: A, central spike; B, F, G, secondary branches; C, tertiary branches; D, whorl of secondary branches; E, a single secondary branch.

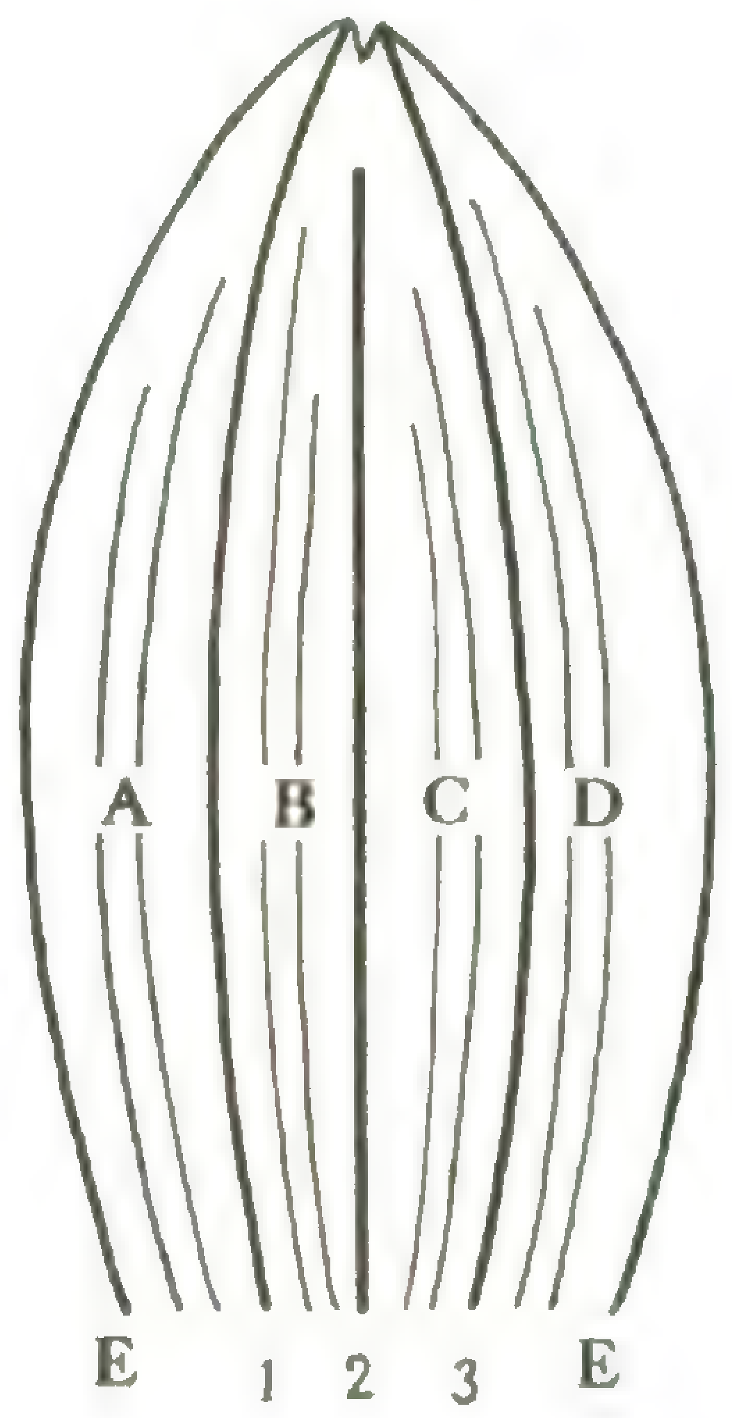


Fig. 2. Semi-diagrammatic glume from a staminate spikelet: 1, 3, keel veins; 2, median vein; A, left margin; B, left shoulder; C, right shoulder; D, right margin; E, edge of glume.

Since a certain variation exists between spikelets in an individual corn tassel, one has to be careful not to confuse this variation *within a plant* with the variation *between plants*. He has always to be sure that the material studied is taken from the same part of the tassel. In the present study this principle has been followed as completely as was possible.

In his study of prehistoric corn tassels from southern Utah, Anderson (1944c) described the general structure of an average corn tassel. His description, which gives a clear picture of the different parts of the male inflorescence and also explains the terminology most commonly used, refers to fig. 1:

> The maize tassel is built upon a primary axis terminated by the CENTRAL SPIKE (A, fig. 1), along which the spikelets are arranged in many rows (in some South American varieties they are in whorls of 3 or more). Below the central spike are the SECONDARY BRANCHES 'B', 'F', 'G' whose number varies greatly in different races of maize. The lowermost secondaries may bear TERTIARY BRANCHES 'C', and in some South American varieties these may even produce branches of the fourth order. The secondaries may arise singly from the main axis (E) or may be in WHORLS (D) of two or more. On the secondaries the SPIKELETS are arranged in pairs, though, as will be shown below, there are departures from this regular arrangement in North American maize. In each pair one spikelet is ordinarily pedicellate and one is sessile, but in North America the pedicellate spikelet may be so subsessile as to be indistinguishable from its neighbor. In South American maize the secondaries often have a long sterile zone at the base of the secondary branches which is without spikelets. In the Southwest and in Mexico this zone is short or is lacking altogether.

In studying the spikelet characters the pedicellate spikelets of the median third of the central spike have been used whenever possible. An exception was the material from Bat Cave, which consisted of fragments of tassels alone, and only a few of these were from the central spike. Here the most representative and most characteristic spikelets were chosen for measurement.

In the glume, especially the lower one, the keel veins and the median vein are more prominent than the others and divide the glume into four distinctive areas (text-fig. 2). To facilitate description these areas have been named *left margin, left shoulder, right shoulder,* and *right margin.* The *shoulder* (B and C) is that part of the glume between the keel veins and is divided by the median vein into two parts, the left shoulder and the right shoulder. The *margin* (A and D) is that part of the glume between the edge of the glume and the keel vein. The veins in the margin are called *marginal veins* and those in the shoulder, *shoulder veins.*

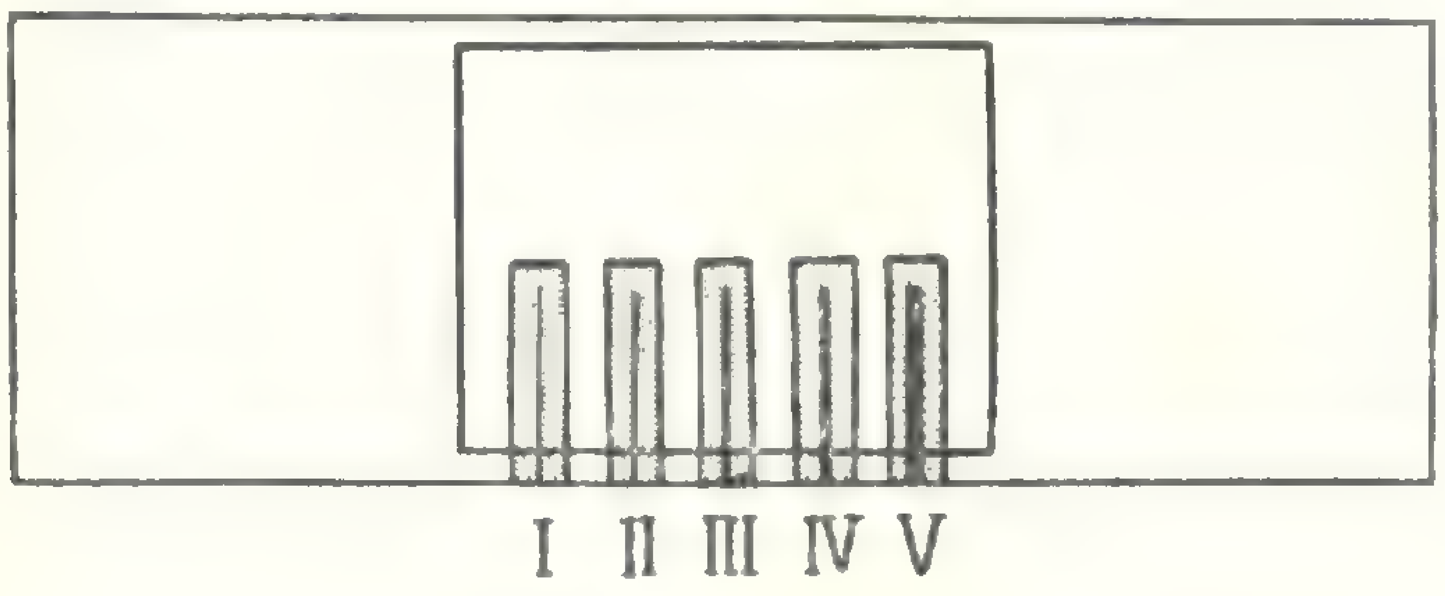


Fig. 3. Diagram of the microscope slide used in scoring the size of the veins in the glumes. When the size of the vein which is to be scored is smaller than I on the standard slide it is designated as O; veins which are as large as I, but smaller than II, are scored as I, and those as large as II but smaller than III are scored as II, etc. Veins as large as V or larger are scored as V.

In order to score the size of the veins, small pieces of glumes containing veins of different sizes were mounted in balsam on the edge of a microscope slide (text-fig. 3). Using this slide as a scale it was possible to classify the veins into six different categories, scored 0 to V inclusive. For the method of scoring see caption of text-fig. 3. The lower glumes from 20 pedicellate spikelets of each variety were measured and scored, using a dissecting microscope with an ocular micrometer. For each glume the following measurements were taken: the lengths of the glume and the median vein, the widths of the left and right margins, and those of the left and right shoulders, the number and sizes of all the veins. It being assumed that it was the averages of the margin widths and of the shoulder widths which were significant, these were computed for each glume measured. Arithmetic means of the measurements for each variety were then made and used in constructing the charts and diagrammatic drawings.

EXPLANATION OF PLATES 2–5

Semi-diagrammatic drawings of average glumes.

Twenty glumes of each variety were measured and scored and the mean values of the results calculated as outlined in the chapter on "Material and Methods." Since the resulting numbers referred chiefly to size, a representative glume most nearly meeting these average measurements was chosen to serve as a pattern for the shape. The drawings were made to the scale 1:15 and were later reduced to one-fifth size.

In each figure (from 1 to 114) the drawing to the left represents the glume shoulder and the one to the right, the right margin of the glume. The differences in vein size are indicated by different widths of lines. For example, in fig. 1, drawing to the left, the sizes of the veins are, from left to right, 3, 1, 0, 2, 0, 1, 3, and in the drawing to the right, 3, 0, 1, 1; and in fig. 13, drawing to the left, the sizes of the veins are 5, 2, 2, 3, 2, 2, 5, and in the one to the right, 5, 2, 3, 2. The number and sizes of the veins, as well as the other measurements, are given in the table in Appendix II.

The drawings on plates 2–5 represent the following varieties:

PLATE 2

1. Arica, Quiani Excavation, Division I, Layer D 1
2. Arica, Playa Miller Excavation, Level ABC
3. Arica, Playa Miller Excavation, Level D 3, No. 1
4. Arica, Playa Miller Excavation, Level D 3, No. 2
5. Bat Cave, VI-128
6. Bat Cave, IV-329-1
7. Bat Cave, IV-280
8. Bat Cave, IV-329-2
9. Bat Cave, V-186
10. Bat Cave, IV-329-3
11. Bat Cave, IV-301-2
12. Turkey
13. Burma
14. India
15. Siam
16. Assam #1074
17. Assam #44
18. Chinese Waxy
19. China #149114A
20. China #149118
21. Argentine Popcorn
22. Río Loa
23. Soledad #5065-2
24. Soledad #5075-3
25. Soledad #5075-5
26. Soledad #5075-1
27. Creole Flint

PLATE 3

28. Bolivia, Mangelsdorf's #127895
29. Coroico #6094-2
30. Valle #6165
31. Titicaca #7700-5
32. Titicaca #7729-2
33. Titicaca #7729-5
34. Manglaralto
35. Quito #8-4
36. Quito #1-6
37. Quito #9-3
38. Quito #4-2
39. Quito #6-1
40. Cuzco #10-2
41. Cuzco #9-2
42. Cuzco #8-9
43. Cuzco #4-3
44. Cuzco #3-1
45. Maíz reventador, Coalcomán
46. Sa 15 b-4
47. Maíz chapolote
48. Talpa
49. Culiacán #1-8
50. Sauer #11-4
51. Maíz reventador, Kelly #3-4

PLATE 4

52. Hackberry
53. Elberta
54. Hickory King
55. Latham's Double
56. Knighton Little Cob Flint
57. Louisiana Gourdseed
58. Tennessee Red Cob
59. Mandan Yellow Flour
60. Harris Mammoth Yellow
61. Fort Kent
62. Dryden
63. Early Quebec Flint
64. Parker's Flint #1
65. Parker's Flint #2
66. 14-row Dakota Flint
67. Longfellow #1
68. Stevens Flint
69. Longfellow #2
70. Tama Flour Corn #1
71. Tama Flour Corn #2
72. Cherokee Indian Corn #1
73. Cherokee Indian Corn #2

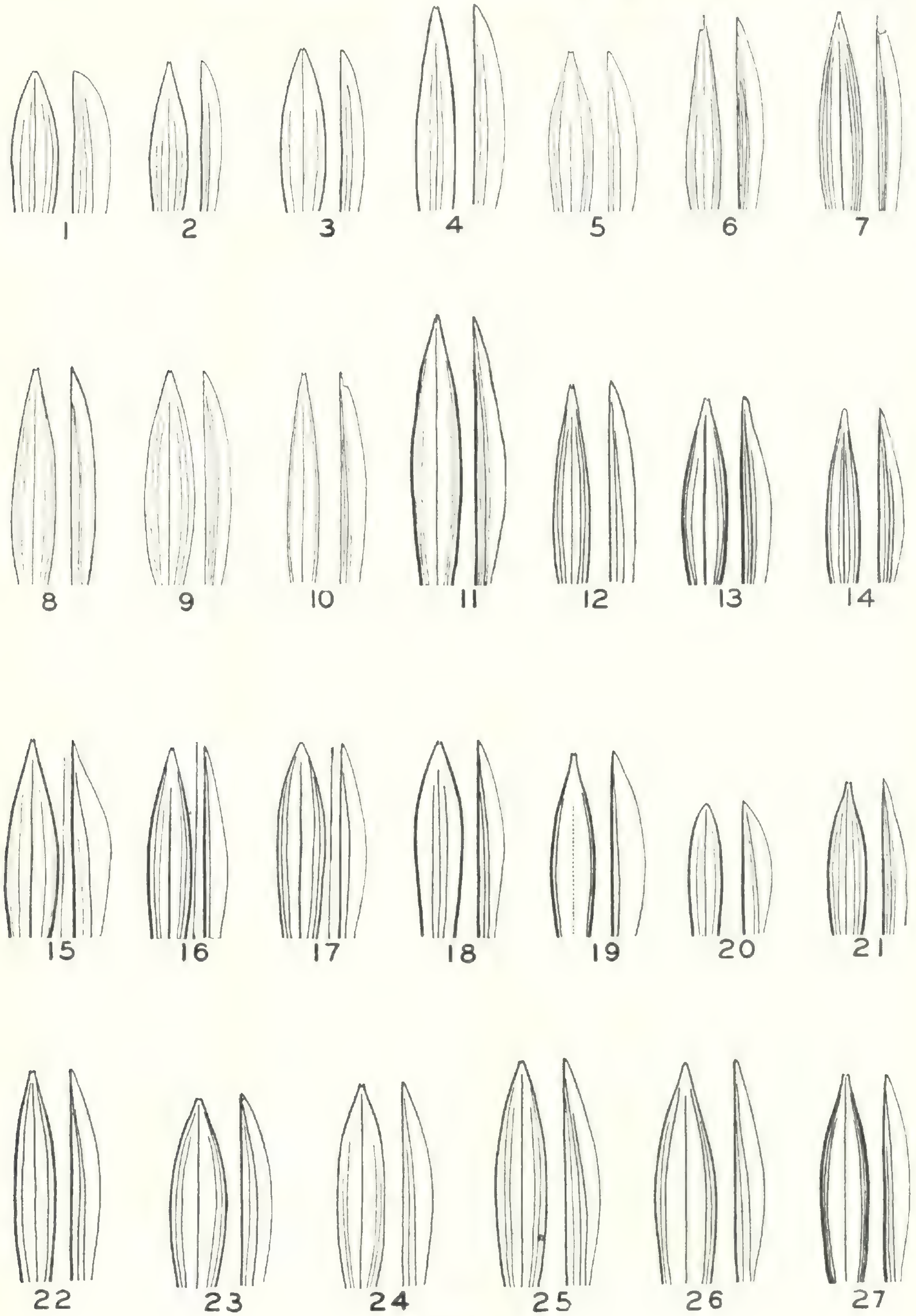


PLATE 2

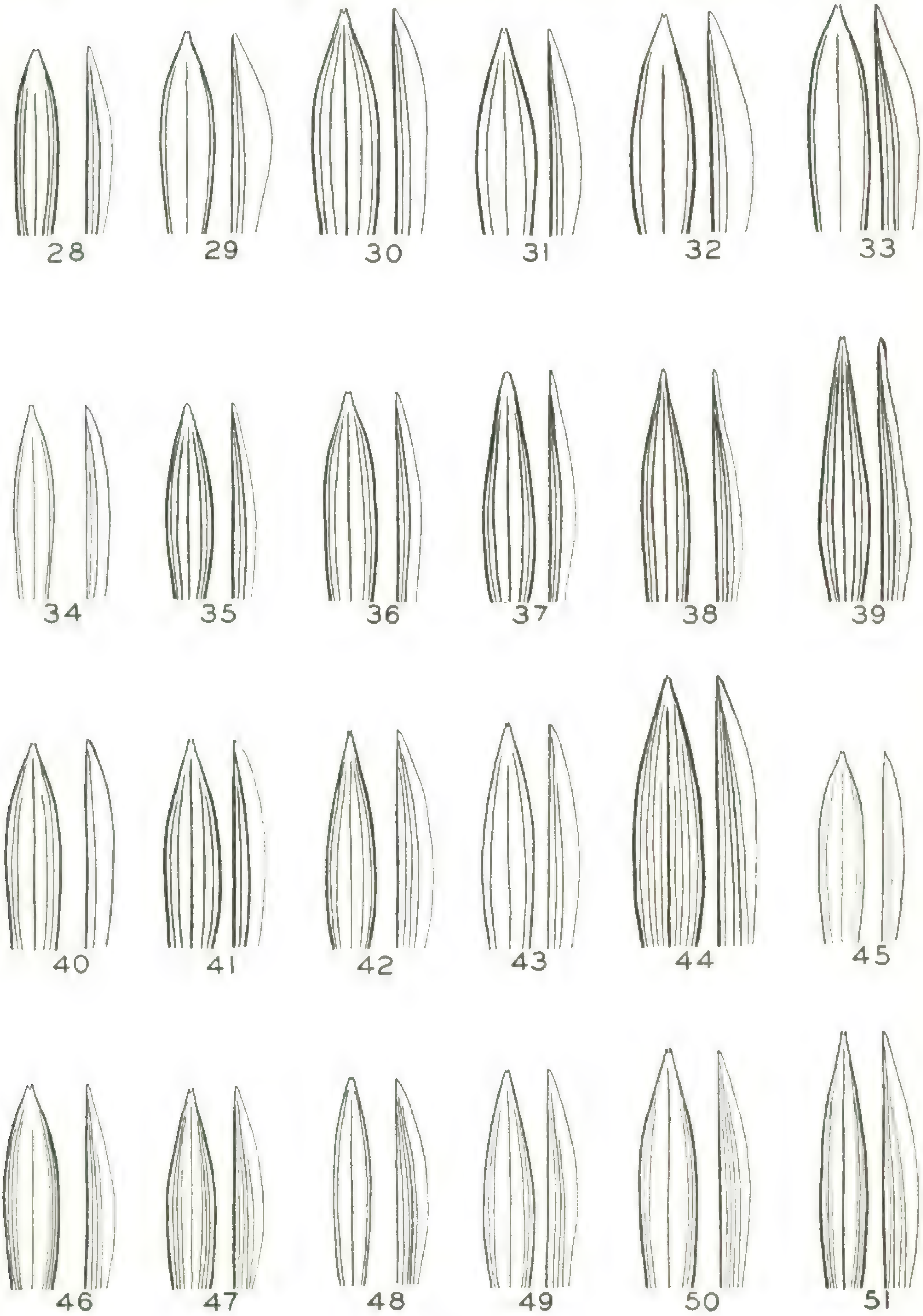


PLATE 3

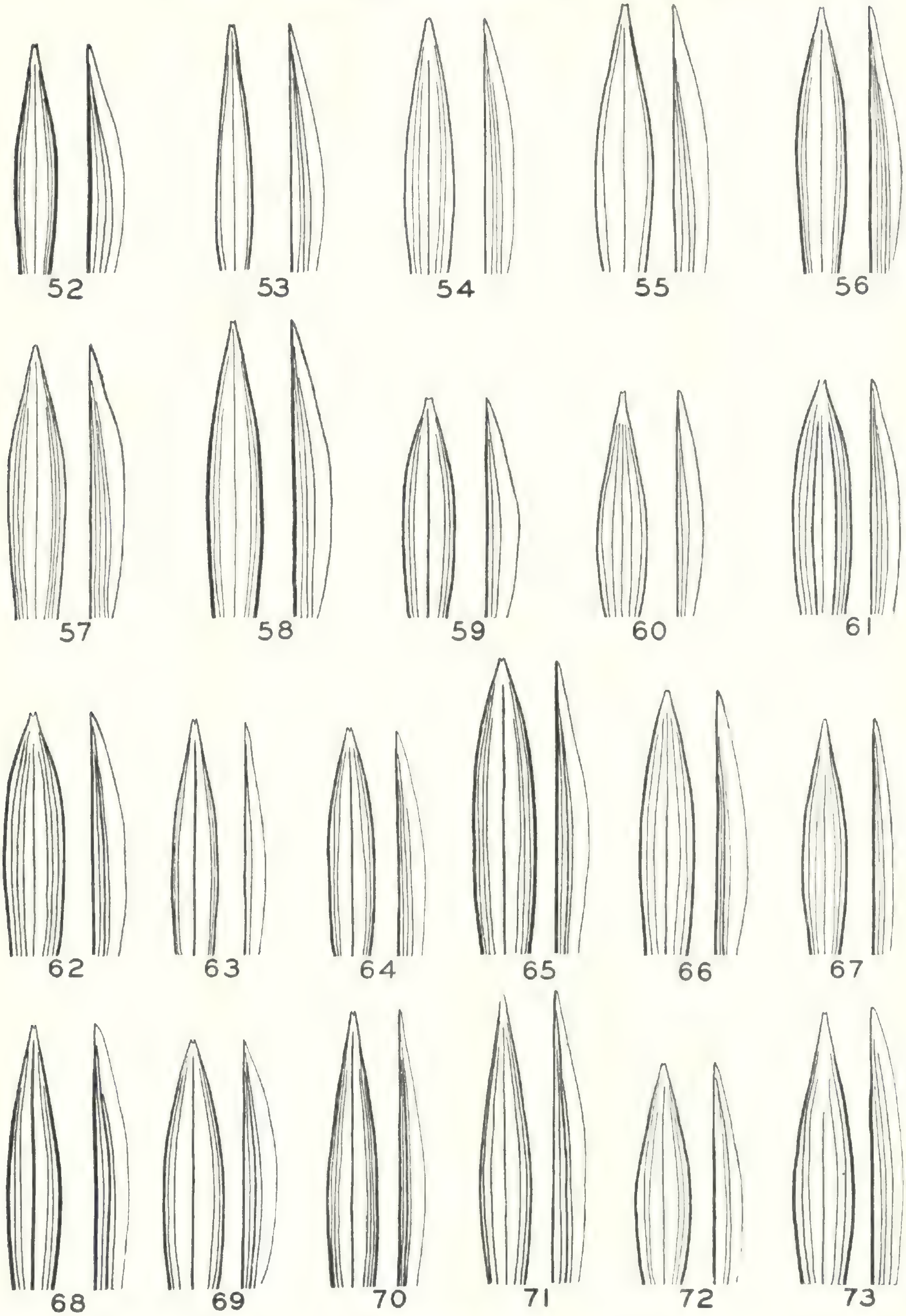


PLATE 4

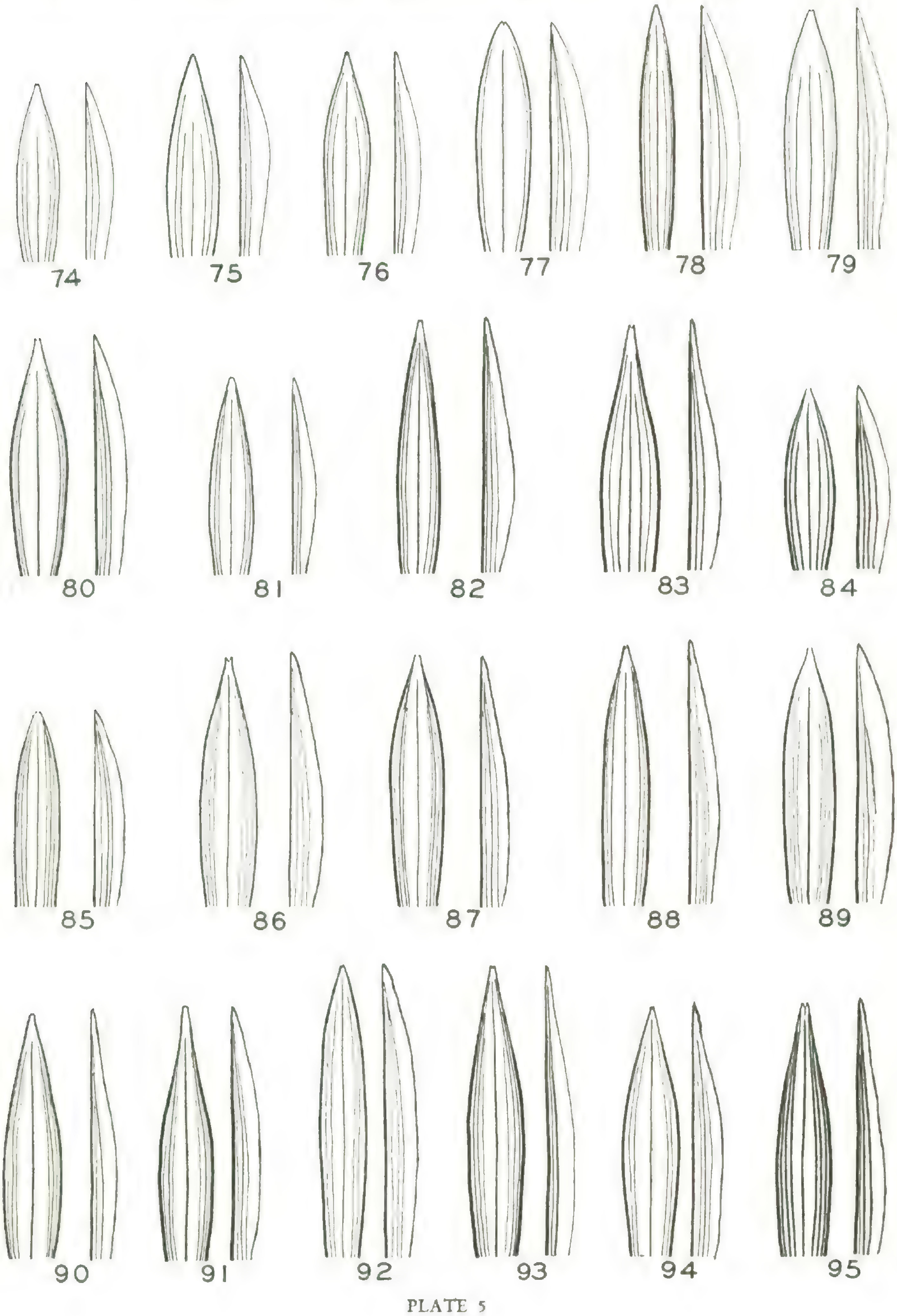


PLATE 5

All the material used in this study is divided into groups according either to geographical distribution or to the similarity of the varieties with respect to different characters. These groups are:

A. Prehistoric maize:	1. Arica 2. Bat Cave
B. South American maize:	1. Old South American Pop Corn 2. Andean Highland maize
C. Central American and Mexican maize:	1. Western Mexican maize 2. Maize from El Capulin and Toluca 3. Guatemalan maize
D. Caribbean maize:	1. Cuban maize 2. Creole Flint
E. North American maize:	1. Northern Flints 2. Papago maize 3. Southern Dents
F. Oriental maize:	Varieties from Assam, Burma, China, India, Siam and Turkey

The exact origin of all these collections is given in Appendix I.

Prehistoric Tassel Material

For understanding variation in the spikelets of modern varieties of maize the discoveries of prehistoric tassels and tassel fragments are of great potential value. In order to understand what changes, if any, have taken place in the entire corn tassel through the centuries the tassels of ancient varieties furnish important objects for comparison. Of several museum collections of prehistoric and pre-Columbian maize tassels, the collection from Arica, Chile (Bird, 1943) and that from Bat Cave, New Mexico (Mangelsdorf and Smith, 1949) have not previously been investigated in detail.

Beginning in 1941, under the sponsorship of the Institute of Andean Research, extensive archeological excavations were made by Mr. Junius Bird at Arica in northern Chile. Among the rather abundant maize remains discovered were four complete and well-preserved tassels, which came from three different levels. The exact age of the deposits at Arica is not yet known but three major periods have been defined, one pottery period and two pre-pottery periods. The second pre-pottery period ended with the beginning of agriculture. Of the material used in this study one tassel, that of the Quiani Excavation, Division I, layer D 1, represents the oldest type; the three others are somewhat younger and are from levels D 3 and ABC of Playa Miller Excavation.

PLATE 5

74. Santa Lucia #3
75. Santa Lucia #6
76. Santa Lucia #4
77. Santa Lucia #2
78. Santa Lucia #1
79. Santa Lucia #5
80. Maíz de Elote
81. Toluca #2
82. Toluca #1
83. El Capulin #1063
84. Chiripo Indian Corn
85. San Andreas
86. Coyote #1
87. Topawa #2
88. Topawa #1
89. Pia Oik #2
90. Kerwo #1
91. Kerwo #2
92. Coyote #2
93. Cold Fields #5
94. Pia Oik #1
95. Papago (Lochiel, Arizona)

In 1948 an expedition from the Peabody Museum of Harvard University made excavations in Bat Cave, Catron County, New Mexico. According to Dr. Ernst Antevs, who determined the age of the material found in Bat Cave, "the cultural deposits containing the maize had their beginning not later than 2500 B. C." (Mangelsdorf and Smith, 1949, p. 217). Arnold and Libby (1951), using the radio-carbon technique, have determined the age of the oldest maize-bearing deposits, the depth of which is three to four feet, as being 2249 ± 250 years, and the age of the youngest deposits, which are up to one foot deep, as being 1752 ± 250 years. Mangelsdorf and Smith, using pottery as an index, had previously calculated that the deposits containing maize remains covered a total span of not less than 3000 years. The radio-carbon technique has, however, shown that the span is probably less than that, the difference in age between the oldest and youngest maize-bearing levels being only 500–1000 years.

The depth of the deposits in Bat Cave in which maize remains have been found averaged between five and six feet. The lowest level, or stratum, was designated as I, and the uppermost as VI (Mangelsdorf and Smith, 1949). Altogether, eight tassel fragments and one rather complete tassel were found. All this material is from the three upper levels, IV, V, and VI. In level IV one tassel (#329-3), three fragments of central spikes (#301-2, #329-1 and #329-2) and two fragments of secondary branches (#301-1 and #280) were found. Level V contained one fragment of a central spike (#186) and a fragment of a lateral branch (#212). In level VI only a fragment of a lateral branch (#128) was found.

In both the Arica and the Bat Cave material the branching of the tassels, as well as the arrangement of the spikelets in the tassels and the fragments, was studied (pls. 7–9). The lengths of the internodes and of the pedicels of the spikelets were measured and are presented to scale as diagrammatic drawings. In the material from Arica the central spike or a portion of it and one or two secondary and tertiary branches (in each case the most characteristic ones for each variety) are represented in the detailed drawings (pls. 7–8). In the material from Bat Cave both the tassel and all the fragments are represented (pl. 9).

EXPLANATION OF PLATE 6

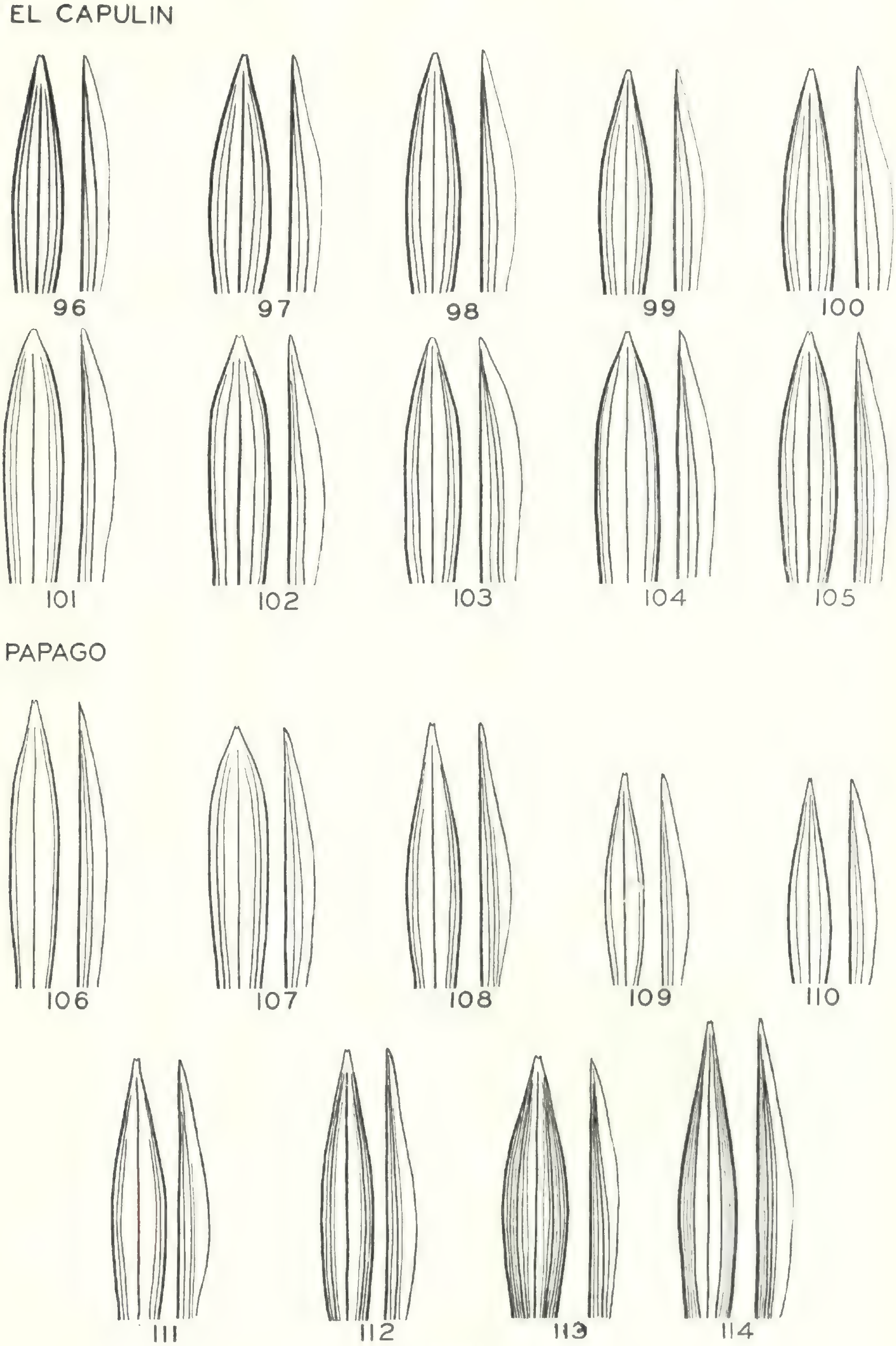
This plate compares variation within the same tassel with that between different tassels in the same field. The upper two rows of figures represent a relatively uniform variety, the lower two rows, an extremly variable one. Measurements, scoring, and construction of diagrams are described in "Explanation of Plates 2–5."

Figs. 96–100. Five individual spikelets from one plant of El Capulin #1059.

Figs. 101–105. Average spikelet of five different plants of El Capulin: fig. 101, #1062; fig. 102, #1059; fig. 103, #1064; fig. 104, #1062A; fig. 105, #1060.

Figs. 106–110. Five individual spikelets of one plant of Papago maize, Chukut Kuk #1.

Figs. 111–114. Average spikelets from four different plants of Papago maize, Chukut Kuk: fig. 111, #1; fig. 112, #2; fig. 113, #3; fig. 114, #4.


EL CAPULIN
96
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PAPAGO
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114

PLATE 6

The Material from Arica

The tassel specimen from the Quiani excavation, Division I, Layer D 1, is the most complete of all the tassels from Arica. It is rather small and in many respects simulates the tassels of certain present-day South American popcorn varieties. At its 7 nodes there are 17 secondary branches, of which the lowermost has again 2 tertiary branches. The longest complete secondary branches are 112–114 mm. in length (pl. 7, fig. 115). The central spike is nearly complete and measures 100 mm. long. Its uppermost and basal thirds are illustrated in figs. 116 and 117. The median third has not been illustrated because of its similarity to the uppermost third. The latter (fig. 116) has 8 nodes, with 3 spikelet pairs at 3 nodes and 2 spikelet pairs at 2 nodes. Of a total of 44 spikelets, 33 are sessile and 11 pedicellate. The lower portion (fig. 117) has 6 nodes at which the spikelet pairs are arranged as follows: 2 nodes with 3 pairs each, one node with 2 pairs, one node with 1 pair, one node with 2 pairs plus 1 spikelet, and one node with 1 pair plus 1 spikelet.

The first secondary branch (pl. 7, fig. 118), which is complete, is 114 mm. long. It has a very short sterile zone, if any. Of the 29 nodes, 27 have but one spikelet pair, and only the 2 nodes toward the tip of the branch have 2 spikelet pairs each. Of a total of 62 spikelets, 34 are sessile, the rest being either pedicellate or subsessile. The two tertiary branches (figs. 119 and 120), both of which have been broken, are attached at the base of the first secondary branch. One of them (fig. 119) contains 12 nodes, the other only 6 (fig. 120). In the shorter tertiary branch there are 4 nodes with one spikelet pair each, and 2 nodes with 4 spikelet pairs each. Of the total of 16 spikelets, 10 are sessile and 6 pedicellate. In the longer tertiary branch there is one spikelet pair at each node; of these 13 are pedicellate and 11 sessile.

Tassel No. 1 from Playa Miller Excavation, Level D 3 (pl. 8, fig. 128) has only 8 secondary branches and 3 tertiary branches at a total of 5 nodes. Since all the secondary and tertiary branches, as well as the central spike, are broken, it is not possible to tell their original lengths. As indicated in fig. 129, the upper half of the central spike has rather short internodes. At 18 of the nodes there is only one spikelet pair, at one of them 2 pairs, while at each of 4 nodes there are 3 spikelet pairs. Of the total of 66 spikelets, 52 are pedicellate, the rest sessile.

EXPLANATION OF PLATES 7 AND 8

Tassel and tassel-branch diagrams of the prehistoric material from Arica, Chile, collected by Mr. Junius Bird. The arrangement of the secondary and tertiary branches was studied by measuring the internodes in that part of the tassel. The lengths of the central spike and of the secondary and tertiary branches were measured. The lengths of the internodes of the central spike or of a part of it and of one or two more representative secondary and tertiary branches were measured as well as those of the spikelet pedicels. Finally, the number of spikelets per node was counted. The detailed diagrams were constructed to the scale 1:10 and later reduced one-fifth (twice natural size). In the drawings the solid ovals represent spikelets which were present on the specimen; the hollow ovals, spikelets which had been lost. If the pedicel were broken, this is indicated by two dots; if the pedicel were still complete, but only the spikelet lost, the missing spikelet is indicated by a hollow oval. Variation in glume length is not indicated.

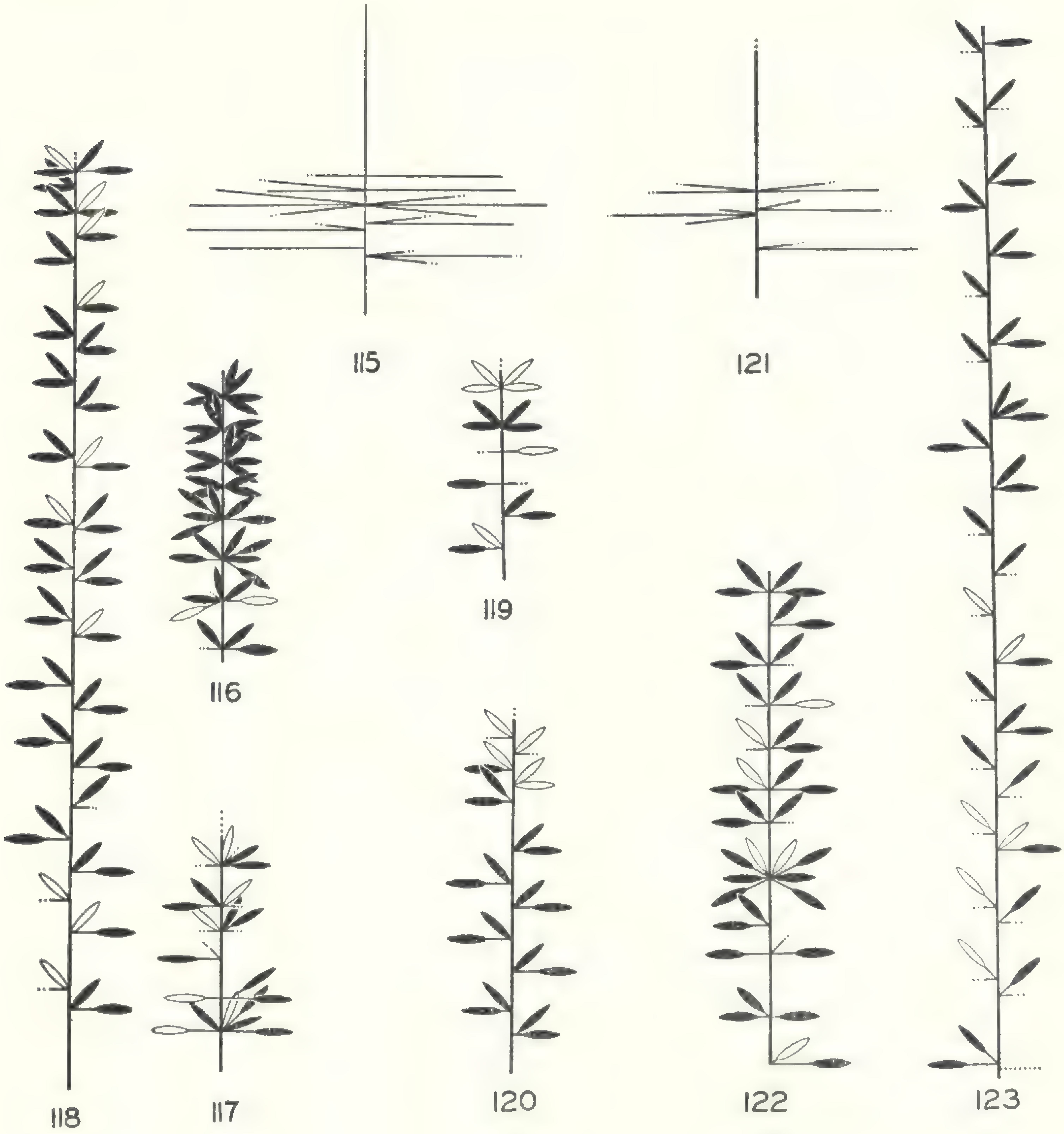
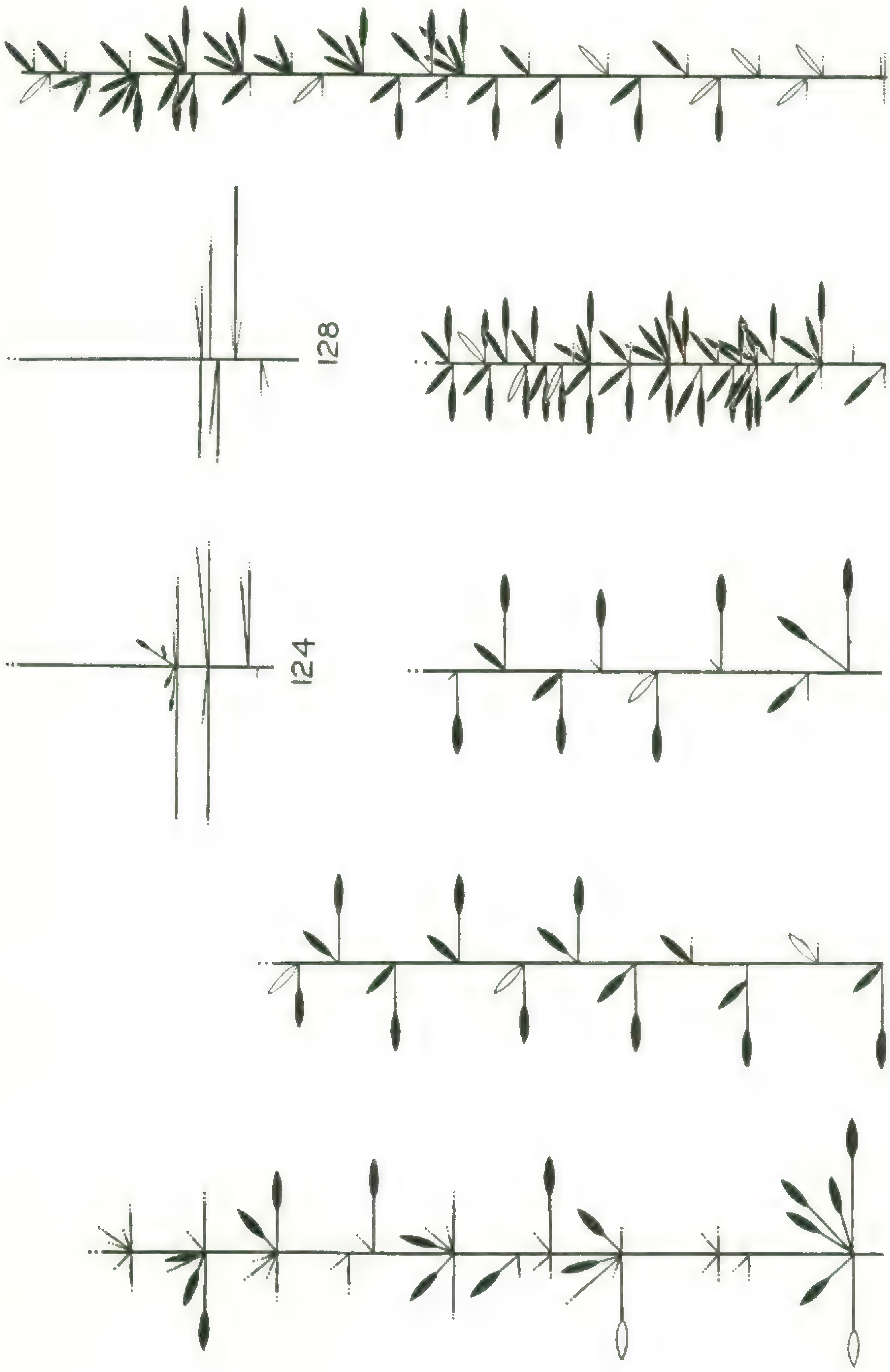


PLATE 7

Figs. 115–120. Quiani Excavation, Division I, Layer D 1:
Fig. 115. The tassel.
Fig. 116. Uppermost portion of the central spike.
Fig. 117. Basal portion of the central spike.
Fig. 118. Lowermost secondary branch.
Fig. 119. Tertiary branch.
Fig. 120. Tertiary branch
Figs. 121–123. Playa Miller Excavation, Level ABC:
Fig. 121. The tassel.
Fig. 122. Central spike.
Fig. 123 Lowermost secondary branch.



130

128

129

124

127

126

125

PLATE 8

The secondary branch (pl. 8, fig. 130) at the base of which the tertiary branches were attached has no sterile zone at the base. Of a total of 29 nodes, at 21 there is one spikelet pair, at one node one spikelet only, and at 7 nodes two spikelet pairs each, the result either of multiplication or of condensation. Of the total of 71 spikelets, 37 are pedicellate and 34 sessile.

Tassel No. 2 from Playa Miller Excavation, Level D 3, consists of 10 secondary branches at 4 nodes (pl. 8, fig. 124). All are broken, the longest branch being now only 9.5 cm. long. At the same node where the uppermost secondary branches are attached there are two spikelet pairs present as well. The broken central spike (fig. 125) has 12 nodes; at 6 of these there are 3 spikelet pairs each, at 2 there are 2 pairs each, and at the remaining 4 there is only one spikelet pair each. All the spikelets except one are pedicellate or subsessile.

The uppermost secondary branch has 11 nodes (pl. 8, fig. 126), at each of which there is only one spikelet pair. Of the spikelets, 14 are pedicellate or subsessile and 8 are sessile. In the lower secondary branch (fig. 127) at each of the 8 nodes there is 1 spikelet pair—13 pedicellate or subsessile spikelets and 3 sessile ones.

The tassel from Playa Miller Excavation, Level ABC (pl. 7, fig. 121) consists of 11 secondary branches at 4 nodes. All the branches, as well as the central spike, are broken except the lowermost secondary branch, which is 114 mm. long. The central spike (fig. 122) has 12 nodes; at one node 4 spikelet pairs, at 6 nodes 2 pairs, at 3 nodes only 1 pair, and at 2 nodes 1 pair plus one extra spikelet. The complete lowermost secondary branch (fig. 123) has 28 nodes; at 26 of them there is only one spikelet pair each, at 1 node only 1 spikelet, and at another node 1 pair plus 1 extra spikelet.

The Material from Bat Cave

In level IV at Bat Cave in New Mexico there were one more-or-less complete tassel and five tassel fragments. Despite the broken tips of the branches and of the central spike, tassel IV-329-3 (pl. 9) still shows that the branching was sparse; at 3 nodes there were only 4 secondary branches altogether; there are no tertiary branches and no sterile zones at the base of the secondary branches. On the central spike, 9 of the nodes are present, and the spikelets are arranged with one spikelet

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EXPLANATION OF PLATE 8

Figs. 124–127. Playa Miller Excavation, Level D 3, No. 2:
Fig. 124. The tassel.
Fig. 125. Central spike.
Fig. 126. Uppermost secondary branch (that to the left in fig. 124).
Fig. 127. Lowermost secondary branch.
Figs. 128–130. Playa Miller Excavation, Level D 3, No. 1.
Fig. 128. The tassel.
Fig. 129. Uppermost half of the central spike.
Fig. 130. Second lowest secondary branch.

pair at each of 4 nodes, 2 spikelet pairs at 1 node, only 1 spikelet at each of 2 nodes, and 1 spikelet pair and a single spikelet at 2 nodes. Of the total 20 spikelets, 2 are sessile and 18 pedicellate with rather long pedicels. Of the uppermost secondary branch there are only 2 nodes left, with 1 spikelet pair at each. The secondary branch to the left has 15 nodes, at 13 of which there is one spikelet pair each; at one node there is a spikelet pair plus a single spikelet, and at another there is only a single spikelet. The secondary branch to the right has 7 nodes, at 5 of which there is only one spikelet pair each and at 2 only a single spikelet each. Of the spikelets, 5 are sessile or subsessile and 7 are pedicellate. The fragmentary lowermost secondary branch has 9 nodes, at 8 of which there is 1 spikelet pair each and at 1 a single spikelet. There are in all 17 spikelets, 11 being pedicellate and 6 sessile or subsessile.

The fragment of a central spike from level IV (IV-329-1, pl. 9) has 4 nodes at each of which there are two spikelet pairs. All the spikelets are sessile. The fragment IV-329-2 is either from a lateral branch or from a central spike, more probably the latter. It has 14 nodes, at 6 of which there is one spikelet pair each, and at each of the remaining 8 nodes there are 2 spikelet pairs. Of the total of 44 spikelets, 23 are sessile and 21 pedicellate.

Fragment IV-301-1 (pl. 9) is from a lateral branch and has 16 nodes. At 5 of these there is one spikelet pair each; at 2 there are 2 pairs each; at 5 there are 1 spikelet pair and a single spikelet each; and at 4 only a single spikelet each. Of the 37 spikelets, 20 are sessile or subsessile and 17 are pedicellate. The central spike fragment IV-301-2 has only 4 nodes, at 2 of which there are 2 spikelet pairs and a single spikelet each, while at one node there is only one spikelet pair. At one of the nodes there are 6 spikelets altogether in 2 sets of 3 spikelets supported by a single pedicel.

From level V we have two fragments of tassels, one of a lateral branch and one of a central spike. The rather long fragment of the lateral branch (pl. 9, V-212), with 22 nodes, has a single spikelet pair at each node except for one at which there is only a single spikelet. At the basal portion of the fragment the spikelet pairs are arranged on one side of the main axis while in the upper portion they are arranged alternately at two sides of the main axis. Of the 43 spikelets 21 are sessile or subsessile and 22 pedicellate.

EXPLANATION OF PLATE 9

Tassel and tassel-fragment diagrams of the prehistoric material from Bat Cave, New Mexico, forwarded by Dr. Paul C. Mangelsdorf. The method of studying this material and making the drawings is the same as that used for making the detailed drawings of the central spikes and the tassel branches as indicated in "Explanation of Plates 7 and 8."

Fragment IV-301-1, from a lateral branch
Fragment V-186, from a central spike.
Fragment IV-329-2, from a lateral branch.
Fragment IV-301-2, from a central spike.
Fragment IV-280, from a lateral branch.
Fragment IV-329-1, from a central spike.
Tassel IV-329-3.
Fragment VI-128, from a lateral branch.
Fragment V-212, from a lateral branch.

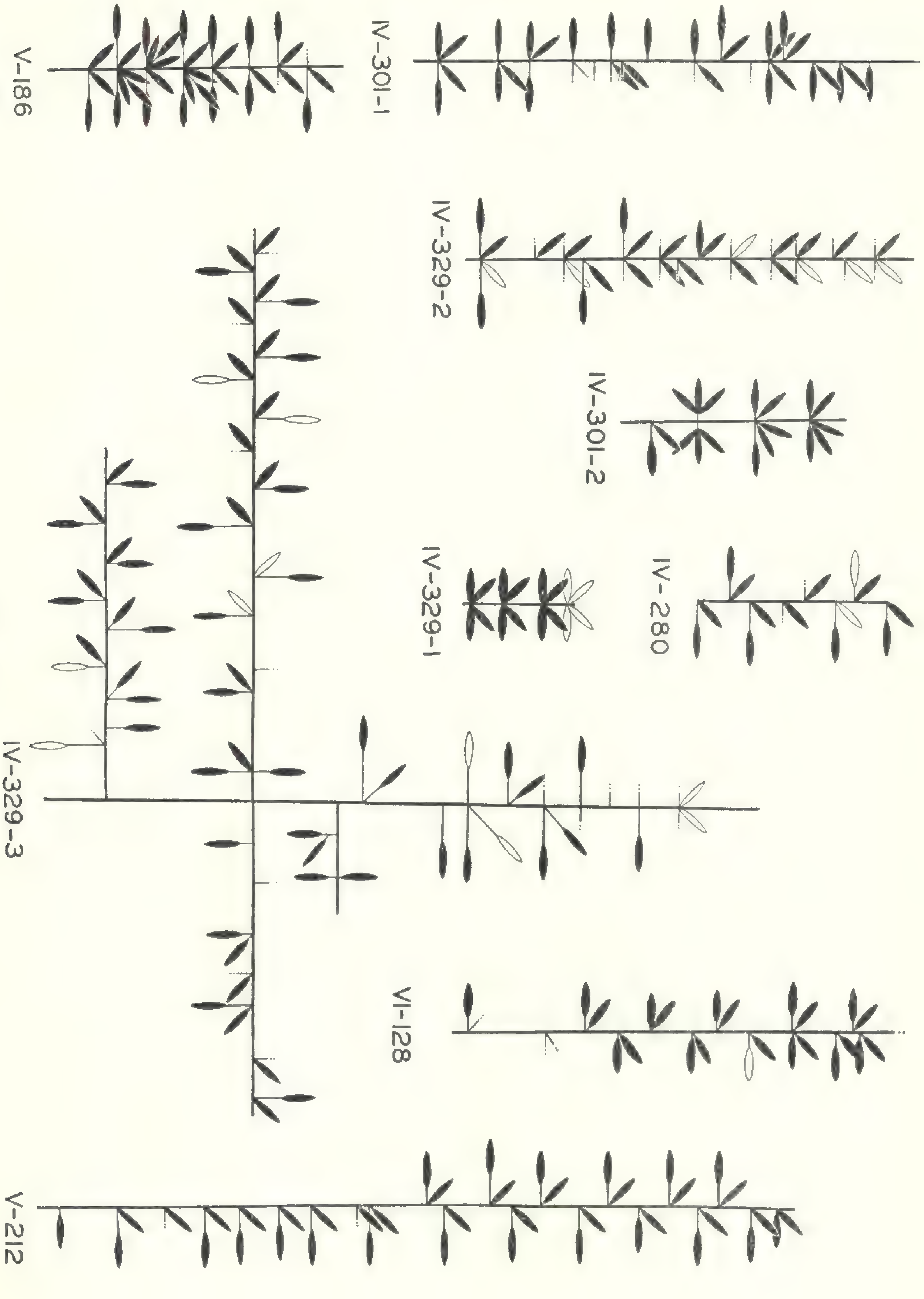


PLATE 9

The fragment of a central spike V-186 (pl. 9) has 8 nodes, with 3 spikelet pairs at each of 3 nodes, 2 pairs each at 2 nodes, and 1 pair and 1 single spikelet at each of 3 nodes. Of the 35 spikelets, 18 are sessile and 17 are pedicellate.

From the most recent stratum, Level VI, there is only one fragment, VI-128 (pl. 9), which is the distal end of a lateral branch. It has 12 nodes, at 11 of which there is one spikelet pair each, at the remaining one two spikelet pairs. Of the spikelets 16 are sessile or subsessile and 8 are pedicellate.

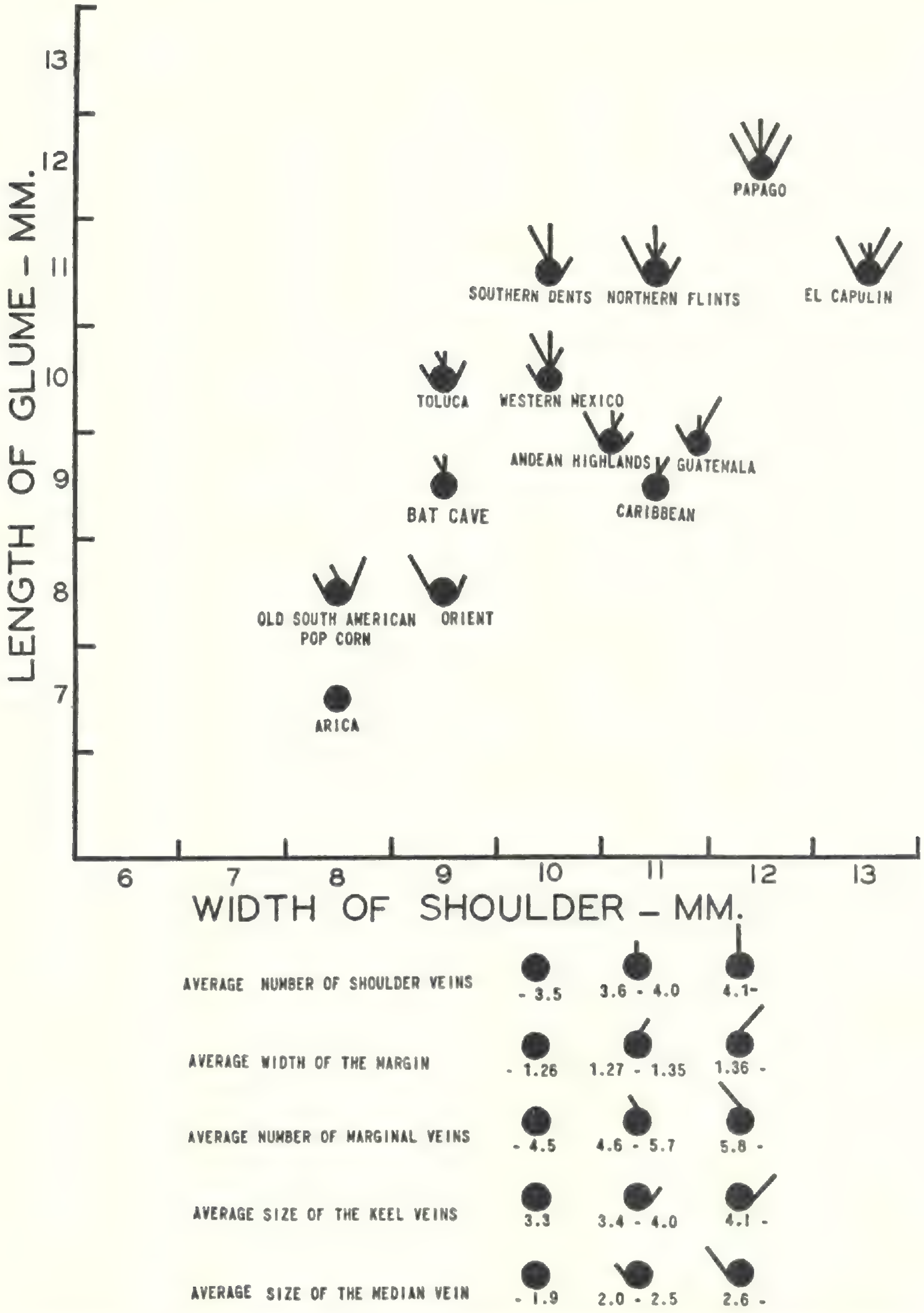
To the extent that any conclusions can be drawn from these few tassels and tassel fragments, the material from Bat Cave seems to be more variable than that from Arica. Of the four tassels from Arica the one we have called tassel No. 2 from Playa Miller Excavation, Level D 3, differs more from any one of the remaining three than these do from each other. It is characterized by long internodes and very long pedicels while the internodes and pedicels of the other three tassels are relatively short, giving the spikes a much denser aspect. Part of this effect may be the result of multiplication.

In the relatively scant material from Bat Cave no such coherent group of tassels can be singled out. The variability among the fragments is as great as that of several different varieties of modern maize. In several fragments there is some suggestion of the condensation which is so common in present-day North American varieties of maize.

Discussion

Maize is a notoriously variable plant. These studies of variation in the male spikelet show that the staminate reproductive organ is no exception to the rule. Not only is there great variation between different varieties and races but also there is striking variation between the spikelets of a single tassel. Spikelet variation is therefore a valuable character, and a study of it seems to give as useful information about the varieties as does any other character. However, studying it is extremely time-consuming. A considerable number of measurements is required since the possible variation within the plant always has to be taken into consideration. Only averages can be used if one is to study variation between plants of a variety or variation between different varieties.

The most important results found here are presented as diagrams, since these give a clear picture of the variation of the material used. In reviewing them certain relationships are suggested which might serve as clues to classification in certain groups. However, until we know more about the interrelationships of the characters depicted here and others previously studied or as yet unanalyzed we cannot say with complete confidence that the suggested clues should form the basis of a final classification. Nevertheless, the results of these spikelet studies seem to correlate with those of previous studies which used different methods and different characters. One of the least variable groups studied is the collection of prehistoric tassels from Arica, Chile. The amount of material is not very large,



Text-fig. 4. Pictorialized scatter diagram showing relationships between variation in 7 different spikelet characters for various groups of maize. (For detailed explanation see p. 90). Each dot represents the mean for 7 measured characters for all the varieties studied in that group; horizontal axis, width of average glume shoulder; vertical axis, length of average glume; five other characters are diagrammed by rays, as explained above.

but it shows at least that three of these four tassel specimens have very similar spikelet characters (figs. 1–3, 115–118, 121–123, and 128–129, pls. 2, 7, and 8). The remaining one of the four tassels varies somewhat from these both in glume and in other spikelet characters (fig. 4 of pl. 2 and figs. 124–127, pl. 8). Among the modern varieties the material from Soledad, Cuba (figs. 23–26, pl. 2), Quito, Ecuador (figs. 35–38, pl. 3), Titicaca, Bolivia (figs. 31–33, pl. 3), and El Capulin, Mexico (figs. 96–105, pl. 6) form similar more or less uniform groups.

The other prehistoric collection, that from Bat Cave, New Mexico, is, on the contrary, extremely variable (pl. 2, figs. 5–11, and pl. 9). Modern Papago maize from Arizona, from the same general area as this prehistoric Basketmaker maize from Bat Cave, is also extremely variable (figs. 106–114, pl. 6). Not only is this variation great between the plants from different fields and different villages (figs. 111–114), but, as shown in figs. 106–110, it is also extremely great within one plant. In this respect it is quite different from the Mexican variety El Capulin (figs. 96–105, pl. 6), which has been taken as a typical example of a uniform variety. In El Capulin both the variation within the plant and the variation between plants from the same field are only slight.

If we take the material of this study as a whole, one of the general effects of the domestication of maize seems to have been an increase in size of the male glume. Apparently, in selecting for larger and larger kernels, man has unconsciously selected for factors which increase the sizes of all the floral parts. However, the increase in spikelet size with increased kernel size is far from being strictly proportional in all kinds of maize. This is strikingly demonstrated by the three kinds of maize, Argentine Pop, Cuzco Flour Corn, and Papago. Of these three, Argentine Pop has both the smallest kernels and the smallest glumes, while Cuzco, with by far the largest kernels, has glumes which are smaller than those of Papago. Ratios of increase in kernel size were found by weighing five kernels of each kind. Corresponding ratios for the glumes were calculated by taking the cube of glume length as a rough measure of volume. The two sets of ratios are as follows:

	Argentine Pop	Cuzco	Papago
Glume	1	2.2	4.9
Kernel	1	25.0	4.0

One sees that the increase in kernel size in Papago maize is accompanied by a roughly proportional increase in glume size, while in the big Cuzco flour corn there has been a great increase in kernel size and only a slight increase in glume size.

EXPLANATION OF PLATE 10

Twelve pictorialized diagrams showing the variation and relationships of 7 measured spikelet characters within each major group of the varieties studied. Each dot represents the average values for one tassel. Horizontal and vertical axes and 5 additional characters scored as in text-fig. 4. On one diagram two similar varieties of Mexican pointed popcorn have been distinguished by solid and open dots.

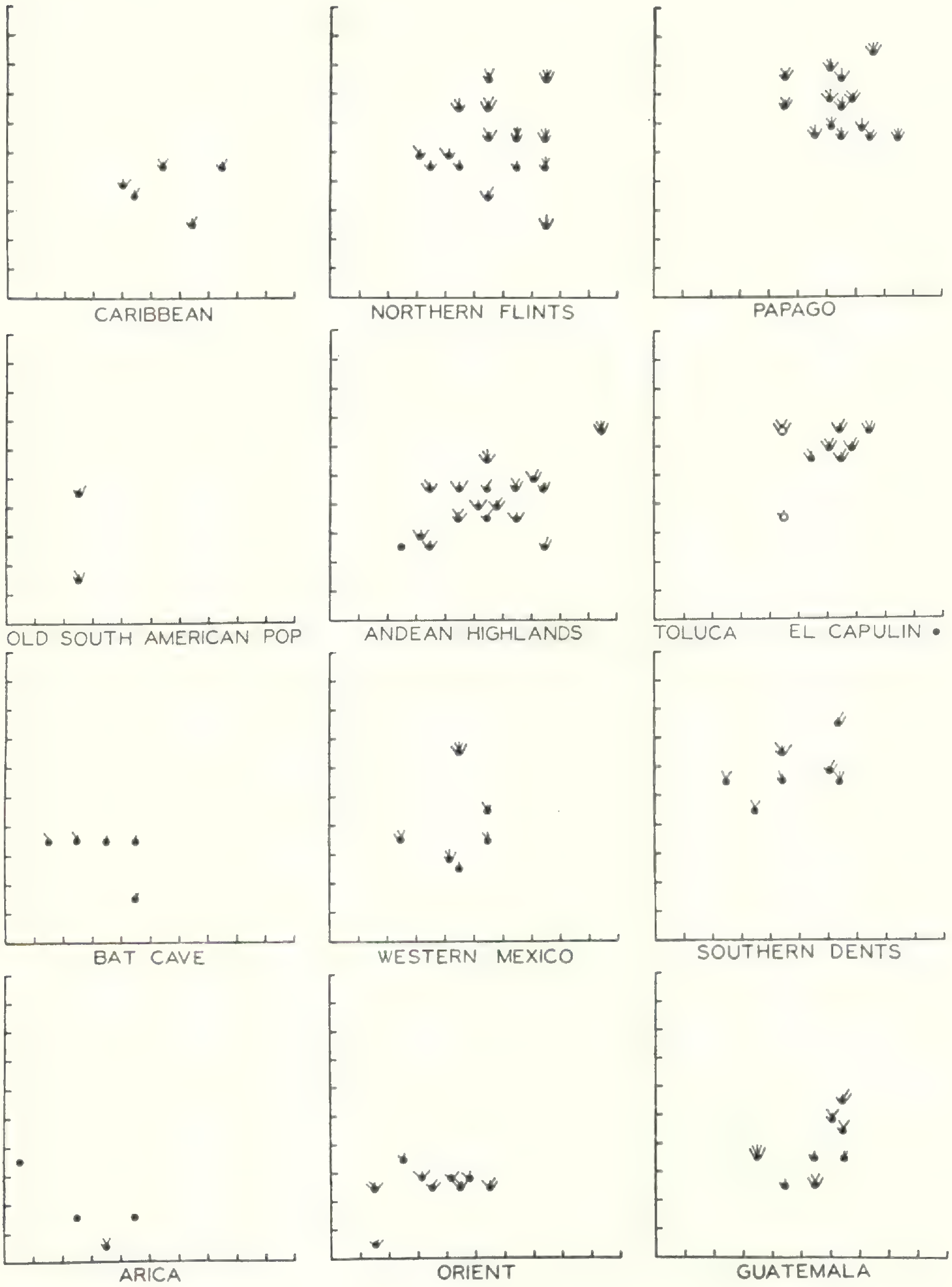

CARIBBEAN
NORTHERN FLINTS
PAPAGO
OLD SOUTH AMERICAN POP
ANDEAN HIGHLANDS
TOLUCA
EL CAPULIN •
BAT CAVE
WESTERN MEXICO
SOUTHERN DENTS
ARICA
ORIENT
GUATEMALA

PLATE 10

The variation of seven characters between different groups of varieties is represented in text-fig. 4. With respect to the groups labelled "Orient" and "Old South American Pop Corn" we note that of their total of 14 characters 9 lie within the range of variation for the corresponding characters of the material from Arica and from Bat Cave. Similar analyses of the North American (including Mexican) groups of varieties shows that in all but one character (with three minor exceptions) the variation from the range for the Arica and Bat Cave material is in the same direction. We may summarize these statements by saying that with regard to the seven characters in question: (1) the material from the Orient and the old South American popcorn varieties are markedly intermediate between the varieties from Arica and those from Bat Cave, and (2) the North American material is not only not intermediate between these two varieties but the variation is almost completely in the other direction.

Summary

An intensive study of variation in the male spikelet of maize was made for the following reasons: (1) Agronomists and ethnobotanists have ignored the male spikelet almost completely because it is of little economic importance. (2) However, for this very reason it has been only indirectly modified by human selection. (3) Experience with wild grasses related to maize points to the male spikelet as one of the most significant features for determining relationships of maize to its possible wild ancestors.

Methods of selecting spikelets for study, for scoring their variation exactly, and for making averages are described in detail. Semi-graphical methods were found most effective in presenting and analyzing the results.

The variation of spikelet and inflorescence characters in prehistoric tassels collected at Arica, Chile, and at Bat Cave, New Mexico, is described in detail. Variation in spikelet morphology was surveyed in the collections of modern maize at the Missouri Botanical Garden.

The following three generalizations can be made:

A. Different strains of maize have characteristically different degrees of variability. The maize of the Papago Indians is morphologically similar to that of the prehistoric Basketmakers and is the most variable in spikelet morphology of any variety in the collection. This extreme variability of Papago maize is shown in variation between different spikelets on the same plant, between averages for different plants from the same field, and between averages of different collections.

B. Central and North American varieties have more and heavier veins, narrower margins, longer and narrower tips, and stronger keels than prehistoric, oriental, and South American varieties. All these differences are in the direction to be expected from the hypothesis of Mangelsdorf and Reeves (1939) that North and Central American varieties have been extensively modified by introgression from *Tripsacum*.

C. Of the prehistoric material that from Arica, Chile, is much more uniform than the greatly variable material from Bat Cave, New Mexico, both in glume characters and in spikelet arrangement. Multiplication is apparently present in the material from Arica and condensation in the material from Bat Cave.

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Appendix I

List of varieties, their origin, and the groups to which they belong. If the varieties were grown outside their natural range, the place is given in parentheses. Explanation of group designations given on p. 77.

1. *Argentine Popcorn:* coll. Parodi, Argentina. (Johnston, Iowa). Group B 1.
2. *Arica:* Arica, Chile. (From the collection of Am. Mus. Nat. Hist.). Group A 1.
3. *Assam:* Naga Hill Tribes, Assam, India. (Gray Summit, Mo.). Group F.
4. *Bat Cave:* Bat Cave, Catron County, New Mexico. (From the collection of Bot. Mus. Harvard Univ.). Group A 2.
5. *Bolivia,* Mangelsdorf's #127895: Bolivia. (Cienfuegos, Cuba). Group B 2.
6. *Burmese Corn:* coll. E. Skarstrom, Telagua, Burma. Group F.
7. *Cherokee Indian Corn:* Cherokee Reservation, North Carolina. (Johnston, Iowa). Group E 1.
8. *China,* #149114 A and #149118: Chengtu, Szechuan, China. (Johnston, Iowa). Group F.
9. *Chinese Waxy:* Shanghai (?), China. (Blandy Exp. Farm, Va.). Group F.
10. *Chiripo Indian Corn:* Costa Rica. (Johnston, Iowa). Group C 3.
11. *Chukut Kuk:* Papago Indian Reservation, Arizona. Group E 2.
12. *Coroico:* Coroico, Alcocha, Bolivia. Group B 2.
13. *Cold Fields:* Papago Indian Reservation, Arizona. Group E 2.
14. *Coyote:* Papago Indian Reservation, Arizona. Group E 2.
15. *Creole Flint:* Southern United States. (Johnston, Iowa). Group D 2.
16. *Culiacán:* Culiacán, Sinaloa, Mexico. (Gray Summit, Mo.). Group C 1.
17. *Cuzco:* Arubamba, Cuzco, Peru. (Arcadia, Cal.). Group B 2.
18. *14-row Dakota Flint:* South Dakota. (Johnston, Iowa). Group E 1.
19. *Dryden:* Northeastern United States. (Johnston, Iowa). Group E 1.
20. *Early Quebec Flint:* Restigouche, Que., Canada. (Johnston, Iowa). Group E 1.
21. *Elberta:* Baldwin Co., Alabama. (Johnston, Iowa). Group E 3.
22. *El Capulín:* El Capulín, Mexico. Group C 2.
23. *Fort Kent:* Northern Maine, United States. (Johnston, Iowa). Group E 1.
24. *Hackberry:* Ozark Mountains, United States. (Arcadia, Cal.). Group E 3.
25. *Harris Mammoth Yellow:* Old United States variety. (Johnston, Iowa). Group E 1.
26. *Hickory King:* Old United States variety. (Ames, Iowa). Group E 3.
27. *India:* India. (Gray Summit, Mo.). Group F.
28. *Kerwo:* Papago Indian Reservation, Arizona. Group E 2.
29. *Knighton Little Cob Flint:* Old United States variety. (Blandy Exp. Farm, Va.). Group E 3.
30. *Latham's Double:* Old United States variety. (Blandy Exp. Farm, Va.). Group E.
31. *Longfellow:* Old United States variety. (Johnston, Iowa). Group E 1.
32. *Louisiana Gourdseed:* Texas, United States. (Gray Summit, Mo.). Group E 3.
35. *Maiz chapolote:* Culiacán, Sinaloa, Mexico. (Gray Summit, Mo.). Group C 1.
36. *Maíz de elote:* coll. Isabel Kelly, Western Mexico. (Arcadia, Cal.). Group C 1.
37. *Maíz reventador:* Coalcomán, Michoacán, Mexico. (Johnston, Iowa). Group C 1.
38. *Maíz reventador:* coll. Isabel Kelly, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
33. *Mandan Yellow Flour:* Northern Great Plains, United States. (Johnston, Iowa). Group E 1.
34. *Manglaralto:* Manglaralto, Ecuador. Group B 2.
39. *Papago:* Lochiel, Arizona. (Johnston, Iowa). Group E 2.
40. *Parker's Flint:* Potsdam, N. Y. (Johnston, Iowa). Group E 1.
41. *Pia Oik:* Papago Indian Reservation, Arizona. Group E 2.
42. *Quito:* Pomasqui, Quito, Ecuador. (Arcadia, Cal.). Group B 2.
43. *Río Loa:* Chiu-Chiu, Chile. (Arcadia, Cal.). Group C 1.
44. *Sa 15 b-4:* Maíz reventador, Jalisco, Mexico. (Blandy Exp. Farm, Va.). Group C 1.
45. *San Andreas,* Cutler's #109: San Andreas Villa Sur, Guatemala. Group C 3.
46. *Santa Lucia:* Santa Lucia, Guatemala. Group C 3.
47. *Sauer's #11-4:* Maíz reventador, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
48. *Siamese Popcorn:* Bangkok, Siam. (La Jolla, Cal.). Group F.
49. *Soledad:* Soledad, Cuba. Group D 1.
50. *Stevens Flint:* Ithaca, N. Y. (Johnston, Iowa). Group E 1.
51. *Talpa:* Talpa, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
52. *Tama Flour Corn:* Tama Indians, Iowa. (Johnston, Iowa). Group E 1.
53. *Tennessee Red Cob:* Old United States variety. (Blandy Exp. Farm, Va.). Group E 3.
54. *Titicaca:* Titicaca, Bolivia. Group B 2.
55. *Toluca:* Toluca, Mexico. (Gray Summit, Mo.). Group C 2.
56. *Topawa:* Papago Reservation, Arizona. Group E 2.
57. *Turkish Popcorn:* Anatolia, Turkey. (Ames, Iowa). Group F.
58. *Valle:* Sucre, Bolivia. Group B 2.

Appendix II

TABLE OF AVERAGES OF MEASUREMENTS FOR TEN CHARACTERS IN TWENTY GLUMES OF EACH VARIETY

Name of variety	Figure number	Average length of glume (mm.)	Average length of median vein (mm.)	Average width of right margin (mm.)	Average width of right shoulder (mm.)	Average number of marginal veins	Average number of shoulder veins	Average size of keel vein*	Average size of median vein*	Average size of right marginal veins*	Average size of right shoulder veins*
Argentine Popcorn	21	7.09	6.91	1.12	0.82	3	2	4	2	1,2,1	1,1
Arica, Quiani Exc. Div. I, D1	1	6.72	6.36	1.36	0.98	3	2	3	2	0,1,1	0,1
Arica, Playa Miller Exc. Layer ABC	2	7.11	5.51	0.99	0.88	2	2	3	1	0,1	1,0
Arica, Playa Miller Exc. Layer D3, #1	3	7.56	6.53	1.07	1.00	2	1	3	1	0,1	0
Arica, Playa Miller Exc. Layer D3, #2	4	9.48	8.00	1.08	0.65	2	1	3	1	0,1	0
Assam #1074	16	8.66	6.87	0.99	0.97	1	2	4	3	1	1,2
Assam #44	17	8.85	7.94	1.18	1.07	1	2	3	3	2	2,2
Bat Cave VI-128	5	7.50	4.75	1.32	1.00	2	2	1	0	0,1	1,0
Bat Cave V-186	9	8.50	8.25	1.17	1.17	3	2	1	1	0,0,0	0,0
Bat Cave IV-280	7	9.25	8.80	1.00	0.98	2	2	1	1	0,1	0,0
Bat Cave IV-301-2	11	12.20	11.70	1.30	1.15	4	3	4	2	0,2,0,0	0,0,0
Bat Cave IV-329-1	6	9.20	8.15	1.12	0.80	4	2	1	0	0,1,0,0	0,0
Bat Cave IV-329-2	8	9.90	9.00	1.02	1.02	3	2	2	1	0,1,0	0,0
Bat Cave IV-329-3	10	9.60	8.20	1.20	0.72	3	1	1	1	0,1,0	0
Bolivia, Mangelsdorf's #127895	28	8.44	6.50	1.13	0.95	2	2	4	4	1,2	3,2
Burmese Corn	13	8.37	7.67	1.28	1.00	3	2	5	3	2,3,2	2,2
Cherokee Indian Corn #1	72	8.77	7.00	1.32	1.32	2	2	4	2	1,2	1,1
Cherokee Indian Corn #2	73	10.15	5.59	1.25	1.22	3	2	5	3	2,2,2	2,3
China #149114A	19	8.30	6.00	1.52	0.92	1	1	4	2	2	2
China #149118	20	6.82	5.87	1.27	0.75	2	1	4	2	1,2	1
Chinese Waxy	18	8.90	7.65	1.17	1.00	2	1	4	2	2	2,2
Chiripo Indian Corn	84	8.37	7.77	1.47	1.12	3	2	5	3	3,3,3	3,3
Chukut Kuk #1	111	12.84	11.70	1.46	1.29	3	2	4	3	2,2,1	2,2
Chukut Kuk #2	112	13.22	12.06	1.92	1.81	3	3	4	4	2,3,1	1,3,2
Chukut Kuk #3	113	12.55	11.86	1.38	1.46	4	6	4	3	1,2,3,2	1,2,3, 1,2,2
Chukut Kuk #4	114	14.39	13.85	1.58	1.36	5	4	5	3	1,1,3, 3,2	3,1,1, 1
Coroico #6094-2	29	9.22	7.87	1.68	1.17	2	1	3	2	2,2	2
Cold Fields #5	93	13.80	13.14	1.29	1.28	2	3	5	3	2,3	1,2,2
Coyote #1	86	11.73	10.90	1.52	1.28	3	3	3	2	1,1,1	1,1,1
Coyote #2	92	13.90	13.49	1.53	1.04	3	2	4	2	1,1,1	1,1
Creole Flint	27	9.63	9.57	1.14	1.04	2	2	5	2	2,2	2,2
Culiacán #1-8	49	10.06	9.14	1.35	1.18	3	2	3	1	1,1	1,2,1
Cuzco #10-2	40	9.31	8.72	1.18	1.20	1	2	4	3	2	2,2
Cuzco #9-2	41	9.32	8.56	1.37	1.19	2	2	5	4	3,4	3,3
Cuzco #8-9	42	9.78	8.55	1.60	1.01	3	2	4	2	2,2,2	2,2
Cuzco #4-3	43	10.26	8.39	1.38	1.10	2	1	3	2	2,2	2
Cuzco #3-1	44	12.30	10.88	1.70	1.52	4	4	5	4	2,3,3, 2	2,2,2, 2
14-row Dakota Flint	66	11.81	10.85	1.31	1.16	3	2	4	2	2,2	2,3,1
Dryden	62	11.12	9.69	1.46	1.28	3	3	4	2	2,3,2	2,2,2

*Scored as in fig. 3.

Appendix II (Continued)

Name of variety	Figure number	Average length of glume (mm.)	Average length of median vein (mm.)	Average width of right margin (mm.)	Average width of right shoulder (mm.)	Average number of marginal veins	Average number of shoulder veins	Average size of keel vein*	Average size of median vein*	marginal veins* marginal veins*	Average size of right shoulder veins*
Early Quebec Flint	63	10.61	9.68	0.86	1.01	1	2	3	3	2,1	2
Elberta	53	11.38	11.29	1.42	0.80	3	1	3	1	1	1,2,1
El Capulín #1059	102	11.93	10.83	1.59	1.36	2	2	5	4	2,3	3,2
El Capulín #1060	105	11.90	10.83	1.47	1.29	3	2	5	4	2,3	3,2
El Capulín #1062	101	12.17	11.04	1.58	1.36	2	2	5	4	2,3	2,2
El Capulín #1062A	104	12.04	11.25	1.64	1.47	2	2	5	3	3,3	3,2
El Capulín #1063	83	11.52	9.79	1.48	1.37	2	2	4	3	2,3	3,2
El Capulín #1064	103	11.77	11.50	1.89	1.32	3	2	4	3	2,3,2	3,2
Fort Kent	61	10.57	9.01	1.36	1.31	3	3	3	2	2,2,2	3,2,2
Hackberry	52	10.55	9.90	1.59	0.92	3	2	3	1	1,2,2	1,1
Harris Mammoth Yellow	60	10.08	8.63	1.19	1.09	2	2	3	2	2,2	2,2
Hickory King	54	11.57	9.73	1.24	1.08	3	2	3	2	1,1	1,1,1
India	14	8.06	7.03	1.13	0.73	3	2	4	3	2,3,3	2,2
Kerwo #1	90	11.94	10.30	1.17	1.36	2	3	4	3	1,2	1,2,1
Kerwo #2	91	12.21	10.45	1.31	1.24	3	3	5	3	1,2,1	1,2,1
Knighton Little Cob Flint	56	13.09	10.97	1.35	1.07	4	2	4	2	1,1	1,1 2,1
Latham's Double	55	12.23	11.28	1.63	1.26	3	1	4	1	1	1,2,2
Longfellow #1	67	10.51	8.42	0.93	0.95	2	2	4	2	1,2	1,2
Longfellow #2	69	11.51	10.72	1.52	1.33	3	2	4	3	2,2	2,3,2
Louisiana Gourdseed	57	12.18	11.56	1.54	1.23	4	3	3	1	1,1,1	1,1, 1,1
Maíz chapolote	47	9.32	8.53	1.26	1.05	4	3	4	2	1,2,2	1,1, 2,1
Maíz de Elote	80	10.98	9.82	1.33	1.26	3	2	4	3	1,2,2	2,1
Maíz reventador (Coalcomán)	45	9.02	8.26	0.95	1.01	2	2	3	1	1,1	1,1
Maíz reventador (Kelly #3-4)	51	11.80	10.97	1.53	1.01	4	3	4	3	1,2,1, 1	1,2,1
Mandan Yellow Flour	59	9.86	9.29	1.43	1.10	2	2	4	3	2,2	2,2
Manglaralto	34	8.85	7.50	1.00	0.85	2	1	2	1	1,2	1
Papago (Lochiel Arizona)	95	12.11	11.40	1.23	1.21	3	3	5	3	2,3,3	3,3,3
Parker's Flint #1	64	10.27	9.44	1.22	0.96	3	2	4	3	2,2	2,2,2
Parker's Flint #2	65	13.25	12.00	1.44	1.38	3	3	5	3	2,2,2	2,3,2
Pia Oik #1	94	11.99	11.30	1.37	1.31	3	2	4	2	1,2,1	1,1
Pia Oik #2	89	11.91	11.03	1.25	1.12	3	3	4	3	1,2,1	1,1,1
Quito #8-4	35	8.80	7.81	0.95	0.95	2	2	4	3	2,3	3,2
Quito #1-6	36	9.35	8.36	1.05	1.12	2	2	4	3	2,3	2,2
Quito #9-3	37	10.23	9.10	1.11	1.09	2	2	4	3	3,2	2,3
Quito #4-2	38	10.45	9.43	1.17	0.99	3	2	4	3	2,3,2	3,2
Quito #6-1	39	11.98	10.79	1.29	1.10	3	2	4	3	2,3,1	3,2
Río Loa	22	9.87	9.68	1.28	0.87	2	1	4	2	2,2	2
Sa 15 b-4	46	9.50	7.41	1.27	1.17	3	3	3	1	1,2,2	2,2,1
San Andreas	85	9.14	8.70	1.28	0.98	3	3	4	3	2,3,2	2,2,2
	78	11.42	10.63	1.75	1.20	3	2	4	2	1,1	1,2,1
Santa Lucia #1	77	10.78	9.26	1.73	1.25	3	1	3	2	1	1,2,1
Santa Lucia #2	74	8.27	6.08	1.21	1.05	2	2	2	2	1,1	1,1
Santa Lucia #3	76	9.54	8.23	1.18	1.11	2	2	3	2	1,1	1,1
Santa Lucia #4	79	10.82	8.66	1.42	1.21	3	2	3	2	2,1	1,2,1
Santa Lucia #5	75	9.50	6.51	1.33	1.25	2	2	3	2	1,1	1,1
Santa Lucia #6	50	10.07	9.90	1.32	1.27	4	2	5	2	1,1	1,1, 1,1
Siamese Popcorn	15	8.90	8.18	1.67	1.17	2	2	4	3	0,2	1,0

Appendix II (Continued)

Name of variety	Figure number	Average length of glume (mm.)	Average length of median vein (mm.)	Average width of right margin (mm.)	Average width of right shoulder (mm.)	Average number of marginal veins	Average number of shoulder veins	Average size of keel vein*	Average size of median vein*	Average size of right Average size of right	Average size of right shoulder veins*
Soledad #5075-1	26	10.32	8.75	1.34	1.39	2	2	3	2	2,1	1,1
Soledad #5075-3	24	9.38	8.97	1.34	1.05	2	2	2	1	0,0	1,1
Soledad #5075-5	25	10.52	9.88	1.58	1.11	3	2	1	1	1,1	1,2,2
Soledad #5065-2	23	8.77	8.39	1.36	1.25	2	2	3	2	1,1	1,2
Stevens Flint	68	12.15	11.43	1.47	1.16	3	2	5	4	2,2	2,3,2
Talpa	48	9.56	8.64	1.36	0.80	4	1	3	3	2	2,2, 3,2,
Tama Flour Corn #1	70	12.73	11.75	1.16	1.08	3	3	4	3	2,2,2	2,3,1
Tama Flour Corn #2	71	13.56	12.00	1.46	1.16	3	2	3	2	2,2	2,3,2
Tennessee Red Cob	58	13.39	13.14	1.68	1.25	3	2	5	1	1,1	1,2,2
Titicaca #7700-5	31	9.46	8.40	1.38	1.31	2	1	4	2	2,2	2
Titicaca #7729-2	32	10.08	7.90	1.81	1.35	2	1	5	3	2,2	2
Titicaca #7729-5	33	10.38	9.14	1.69	1.27	3	1	4	2	2,3,2	2
Toluca #1	82	11.77	10.69	1.45	0.97	3	2	4	3	2,2,1	2,2
Toluca #2	81	9.14	8.07	1.07	0.99	2	2	3	2	1,2	1,1
Topawa #1	88	12.10	10.83	1.41	1.02	4	2	4	2	1,1, 1,1	2,1
Turkish Popcorn	12	9.23	7.15	1.17	0.81	2	2	3	2	2,2	2,2
Valle #6165	30	10.15	9.49	1.30	1.36	2	2	4	2	2,2	2,2

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Volume XXXIX Number 2

Annals of the Missouri Botanical Garden

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PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price	$10.00 per volume
Single Numbers	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Annals

of the

Missouri Botanical Garden

Vol. 39 MAY, 1952 No. 2

THE INDUCTION OF PARTHENOCARPY IN PETUNIA[1]

HENRY A. McQUADE

Numerous attempts to induce haploidy in plants have been made in the past, and the techniques have varied widely. These have included, among other methods, hybridization, both intergeneric and interspecific (Clausen and Mann, 1924; Gaines and Aase, 1926); cold and heat treatments (Blakeslee et al, 1922; Belling and Blakeslee, 1927; Randolph, 1932); injury to plant parts (Davis, 1931; Ivanov, 1938); irradiation of pollen with x-rays (Katayama, 1934; Ivanov, 1938; Rick, 1943); application of various sorts of pollen (Belling and Blakeslee, 1927; Jörgensen, 1928); and chemical treatments (Gustafson, 1936, 1942; van Overbeek et al, 1941). This report is concerned with three of these methods as they affect fruit development: the application of different pollen types and chemical and x-ray treatments. The plants from seed produced in the x-ray experiments will be dealt with in a later report.

PARTHENOCARPY INDUCED BY VARIOUS POLLENS

The effects of pollen extracts have been of some interest since the work of Fitting (1909) and Laibach (Laibach, 1933; Thimann, 1934). Redinger (1938) reported the production of homozygous diploids in *Petunia* through the application of pollen of closely related solanaceous forms. It was decided for this study to apply some pollen from plants bearing no close relationship to *Petunia* as well as some from closely related genera. Table I gives the results obtained.

Materials and Methods.—*Petunia* flowers were emasculated and pollinated with "foreign" pollen. Except where orchid pollinia were used, contamination was prevented by placing a piece of soda straw closed at one end with Scotch tape over the stigma and style. This could not be done with the pollinia for danger of dislodging them. All pollinia from a single orchid bloom were used in each

[1] This study was made possible by a grant from the Blewett Fund of the St. Louis Board of Education. Thanks are due also to Dr. George T. Moore, Director of the Missouri Botanical Garden, and Dr. G. A. L. Mehlquist, Research Horticulturist, for the facilities of that institution; and to Dr. Hugh M. Wilson, Director, and Dr. William B. Seaman, of the Mallinckrodt Institute of Radiology, School of Medicine, Washington University, St. Louis.

treatment. The ovaries were allowed to remain on the plant until dried. After harvest, the thickness, texture, and shape of the ovary walls and activation of the ovules were examined under the binocular microscope and compared to those of normal fruits. Measurements were made along the long and short axes in millimeters. Controls were not pollinated after emasculation but stigmas and styles were covered. Only those treatments which gave positive results are cited below.

Treatments with orchid pollen.—Since the experiments of Fitting and Laibach, orchid pollen has been credited with containing relatively large amounts of some substance or substances, or the precursors of such substances, which initiates development of the ovary.

TABLE I

Pollen sources	Petunia strains pollinated											
	1A	2	2A	3	4	6	LaPal*	BT	Son	Noc	Total	Results
	Number of times used											
Cattleya Mossiae plus stigmatic substance						1					1	—
Stigmatic substance of *Cattleya Mossiae*					4	1					5	—
Cattleya "Priscilla" plus stigmatic substance				3	4	6					13	1+
Cymbidium sp.				16	11		2				29	4+
Cymbidium plus stigmatic substance				7	7	7					21	6+
Delphinium sp.	1	4		1					1		7	—
Lilium longiflorum	2	4	1	8		1					16	—
Lilium tigrinum	8		9	11	8	8	1	8			53	—
Paeonia sp.		6									6	—
Philadelphus sp.	1		2	4	6	2	2	1		1	19	—
Lycopersicum esculentum	1	5	3		1		5				15	—
Nicotiana affinis	1	10	4	9	19	26	7	18			94	4+; 5PF
Nicotiana glutinosa				10							10	—
Nicotiana Tabacum				15							15	1+
Salpiglossis sp.				45							45	2+; 1PF
										Total	349	

*Symbols: LaPal = La Paloma.
BT = Better Times.
Son = Sonata.
Noc = Nocturne

PF = Parthenocarpic fruit.
+ = Some activation.
— = No activation.

Results.—No parthenocarpic fruits were produced. Eleven of the treated ovaries showed mild activation, ten in the form of thickness and texture changes in the upper one-third to one-half of the wall. There was no increase in size. Only in one case was there any activation of the ovules. This ovary exhibited a texture and thickening change in the upper half of the walls (pl. 11, fig. 1), while two ovules at the top of the column developed sufficiently to be classified as distorted empty seeds.

In general, the activation of *Petunia* ovaries with orchid pollen appears to be very slight. It seems possible to bring about such slight activation in the walls without affecting the ovules. In the case where the ovules were activated, the orchid pollinia were accompanied by stigmatic substance.

Treatments with pollen of Nicotiana affinis.—Of the four activated ovaries, one showed a partial hardening of the upper one-third of the ovary wall; three showed a hardening in the upper tip of the wall accompanied by a slight activation of a few ovules at the top of the column. The five parthenocarpic fruits were smaller than normal fruits (5 × 3½ mm., 4½ × 4, 4½ × 3, 3½ × 3, 3 × 3). All the walls exhibited the thickness, texture, and shape of normal fruits (pl. 11, fig. 2). They contained hollow seeds and split when ripe. Two of these fruits contained some ovules which had apparently undergone lesser degrees of stimulation and had developed in some cases to flat and distorted integumental structures (pl. 12, fig. 2).

Treatments with Nicotiana Tabacum.—One ovary showed a hardening and thickening in the upper third of the walls; the ovules were unchanged.

Treatments with Salpiglossis pollen.—Three ovaries gave positive results. In two of these the upper one-third of the capsule showed a hardening on the outside; the inner surface was not shiny as in a normal mature fruit. Neither was any larger than an unpollinated ovary allowed to dry on the plant (2½ × 1½ mm., 3 × 1½). The size of the third fruit (4½ × 3½ mm.) indicated greater activity. The upper three-fourths of the wall had hardened and thickened; the inner surface had become somewhat shiny but ovules showed no activation.

PARTHENOCARPY INDUCED WITH 2, 4-D

The effectiveness of 2, 4-D in the production of parthenocarpic fruits has been amply demonstrated (Avery, 1947). Of the chemical substances used in this study in attempts to stimulate development of the egg, 2, 4-D, although giving no results parthenogenetically, did produce some interesting results parthenocarpically. In an initial test, 2, 4-D at 2 p.p. 100 in lanolin was applied to the stigmatic surfaces of 21 emasculated flowers and in all cases gave positive results. For the most part, these fruits were perfectly normal in appearance, splitting at maturity to reveal an abundance of hollow seeds. A few of these seeds, when punctured with a needle, were seen to have a small amount of whitish material inside. The three largest fruits measured 7 mm. along the long axis and 4 mm. along the short; the remainder showed a gradual decrease in size to the smallest which was 3½ × 2½ mm. Only one of these fruits (6 × 4 mm.) did not contain at least a few empty seeds, but contained only ovules which had obviously undergone an activation where development of the integument had fallen short of the hollow-seed stage.

Because of the pronounced effect of 2, 4-D at such a high concentration, it seemed advisable to check it at lower levels and in different media; accordingly, tests were run using the substance in lanolin, water and talc at concentrations of

1 p.p. 100,000, 1 p.p. 10,000, 1 p.p. 1,000, 1 p.p. 100 and 2 p.p. 100 in each medium.

Materials and Methods.—The pure acid was ground and mixed in lanolin or talc to the desired concentration; when water was used as a medium the material was dissolved in a few cc. of acetone and then properly diluted with distilled water. The paste, powder, or liquid was then applied to the stigmatic surfaces of emasculated flowers; contamination by pollen was prevented by the straw method.

TABLE II

Strain No.	Size (mm.)	Result	Ovules	Change in ovary walls
	2, 4-D in lanolin 1 p.p. 1000			
6	2½ × 1½	—	—	—
6	3 × 2½	Small PF	Some activated	Th, Tex, S
6	3 × 2½	Small PF	1 Hol. S, remainder activated	Th, Tex, S
6	5 × 4	PF	Hol. S	Th, Tex, S
6	4 × 2	Small PF	Activated	Th, Tex, S*
6	3½ × 3	Small PF	Hol. S	Th, Tex, S
6	4½ × 3	Small PF	A few Hol. S (distorted)	Th, Tex, S (upper ¾* of length, papery below)
6	3½ × 2	Small PF	Some activity opposite active part of wall	Th, Tex, S (upper ¾* of length, papery below)
6	3½ × 1½	Small PF	As above	As above*
6	3 × 2	Small PF	As above	As above*
	2, 4-D in lanolin 1 p.p. 100			
6	3½ × 1½	—	—	—
3	4 × 2½	—	—	—
6	3 × 2	—	—	—
6	4 × 1½	—	—	—
6	4 × 3	Small PF	Some activity opposite active part of wall	Th, Tex, S upper ¾*, papery below
6	6 × 4	PF	Some Hol. S, remainder active	Th, Tex, S
6	7 × 5	PF	Abundant Hol. S	Th, Tex, S
6	9 × 5½	PF	Some small round Hol. S, remainder active	Th, Tex, S
6	10 × 5	PF	Abundant Hol. S	Th, Tex, S
6	8 × 5	PF	Abundant Hol. S	Th, Tex, S
6	8 × 4	PF	Abundant Hol. S	Th, Tex, S
	2, 4-D in lanolin 2 p.p. 100			
6	3½ × 1½	—	—	—
6	2½ × 1½	—	—	—
6	3½ × 1½	—	—	—
6	6 × 5	PF	Abundant Hol. S	Th, Tex, S
6	7 × 6	PF	Abundant Hol. S	Th, Tex, S
6	7 × 6	PF	Abundant Hol. S	Th, Tex, S
6	6½ × 6	PF	Activated	Th, Tex, S
3	4½ × 4	Small PF	Activated	Walls soft

Abbreviations: Th = thickness; Tex = texture; S = shape; Hol. S = hollow seed (integument only); PF = parthenocarpic fruit; * = ovules merely activated.

Analysis of the fruits was carried out as before. Controls were treated with lanolin, talc, water, and water and acetone. Most of the plants used were of strain No. 6 but a few flowers of strains Nos. 3 and 4 and La Paloma were treated.

Treatments with 2, 4-D in lanolin.—At concentrations of 1 p.p. 100,000 and 1 p.p. 10,000 there were no positive results. The largely positive effects of the higher concentrations are given in Table II.

Treatments with 2, 4-D in talc.—At concentrations of 1 p.p. 100,000 (eleven stigmas treated), 1 p.p. 10,000 (fourteen stigmas treated), and 1 p.p. 1,000 (ten stigmas treated), no activity was observed. Of the eleven flowers treated at 1 p.p. 100, three responded, while in the ten flowers of the "2 p.p. 100" class, two indicated positive results. Table III deals only with the five positive results obtained.

TABLE III

Strain No.	Size (mm.)	Result	Ovules	Change in ovary walls
		2, 4-D in talc, 1 p.p. 100		
4	6½ × 4	PF	A few activated at top of column	Th, Tex, S
6	4½ × 2	Small PF	Activated	Th, Tex
6	3 × 1½	+	Active at tip of column	Th, Tex, upper ⅓ papery below
		2, 4-D in talc, 2 p.p. 100		
6	5 × 2½	Small PF	Upper ⅓ of column with small distorted Hol. S	Upper ⅔ Th, Tex, S, papery below
6	4 × 2	Small PF	Upper ⅓ of column active	Upper ½ Th, Tex, papery below

Treatments with 2, 4-D in water.—At 1 p.p. 100,000, twelve treated flowers gave no response. Three of eleven flowers treated at 1 p.p. 10,000, two of twelve flowers treated at 1 p.p. 1,000, one of eight flowers treated at 1 p.p. 100, and four of eleven flowers treated at 2 p.p. 100 gave positive results which are summarized in Table IV.

Concentrations of 1 and 2 p.p. 100 in lanolin gave by far the best results of the 2, 4-D treatments, but it seems unnecessary to go beyond 1 p.p. 100 (pl. 11, fig. 3). The resulting fruits ripened on the plant and split longitudinally, as do normal fruits, upon drying. They contained hollow "seeds"; that is to say no endosperm or embryo was present. These seeds are composed of ovular tissue, the integument, which apparently has been stimulated; they are normal in appearance except that they are usually smaller than true seeds and are often somewhat lighter

in color although they may be of characteristic darkness. The pattern of the normal seed coat is always apparent (pl. 12, fig. 3). There was no injury to plant parts through the lanolin mixture.

The poor results obtained with talc mixtures can probably be accounted for by the lack of solubility; apparently where positive results were obtained the stigma was unusually moist. No injury was manifest through talc treatments. The aqueous treatments, on the other hand, produced injury in twelve of the nineteen treated flowers in the classes 1 and 2 p.p. 100. Injury ranged from a single sepal with necrotic spots to complete browning of sepals and pedicel. There can be no doubt that injury is important in reducing the incidence rate of parthenocarpy in these groups. In addition to injury, another difficulty in using water as a medium is that it is extremely difficult, if not impossible, to confine the mixture to the stigmatic surface.

TABLE IV

Strain No.	Size (mm.)	Result	Ovules	Change in ovary walls
		1 p.p. 10,000		
4	5 × 4	Small PF	Activated	Th, Tex*
LaPal	3 × 1½	+	Slight activity	Upper ½ Th, Tex
LaPal	3½ × 2	+	Activity doubtful	Upper ½ Th, Tex
		1 p.p. 1,000		
LaPal	7 × 4	PF	Activated	Th, Tex, S
6	5 × 2	Small PF	Slight activity	Walls soft but capsule splitting*
		1 p.p. 100		
6	6¼ × 4½	PF	Hol. S	Th, Tex, S
		2 p.p. 100		
4	4 × 3	Small PF	Strong activity	Th, Tex
4	7 × 5	PF	Strong activity at top of column	Th, Tex, S
4	4 × 3	Small PF	No activity	Th, Tex
6	7 × 5	PF	Abundant Hol. S	Th, Tex, S

*Ovules merely activated.

PARTHENOCARPY IN X-RAYED OVARIES

Materials and methods.—No. 6 plants were supported so that the flowers rested on a ring covered with Scotch tape. The flowers were strapped in place with Scotch tape on either side of the ovary, care being taken to center the ovary under the target. The technical factors were target distance 15 cm., filter ½ mm. of aluminum, 120 KV, 10 milliamps, H.V.L. = 1.6 mm. of aluminum. Ovaries were treated with 2400, 3000, 3600, 4200, 4800 and 5400 r; the number of fruits

harvested at maturity in each dosage class was 12, 7, 7, 7, 12 and 7, respectively. Untreated pollen from La Paloma flowers was used; contamination after pollination was prevented.

Results.—There was considerable variation in the effect of radiation on the ovule as far as seed development was concerned. In the "2400 r" class fruits contained filled seeds, partially filled seeds, empty but normal-appearing seeds, highly distorted empty seeds, and ovules showing only signs of initial development. Low levels of ovule activation are difficult to assess because there is no way as yet to determine whether an ovule is arrested in development because of radiation damage or whether it simply did not receive enough growth substance following pollination.

Only two fruits in the "3000 r" class contained some filled, partly filled, and round empty seeds. The remainder contained highly distorted ovular structures and ovules indicating little or no activation.

Three fruits of the "3600 r" class contained some filled, partially filled, and empty seeds. Some of these seeds were found to contain a soft, milky material. The remainder contained highly distorted empty seeds and activated or inactivated ovules (pl. 12, fig. 4).

The fruits of the remaining classes (4200, 4800, and 5400 r) contained only distorted empty seeds and ovules at various stages of activation.

Table V gives the results of a germination test conducted in constant illumination of 100 foot-candles supplied by fluorescent "daylight" bulbs and temperature of 25° C. Seeds were sterilized in 3 per cent hydrogen peroxide and germinated in Petri plates on filter-paper moistened with Vickery's solution. Counts were made eleven days after sowing. A germination test is hardly a suitable index of x-ray damage since seeds that germinate may give rise to seedlings that die somewhat later. Furthermore, this test cannot be regarded as definitive because of the small number of seeds per sample.

TABLE V

Dosage r	Seed number per sample	Sample wt. (mg.)	Full germination to 2 cotyledons	Laggards	Total
2400	100	7.29	7	8	15
3000	100	6.39	5	3	8
3600	75	4.22	2	3	5
Control	100	11.48	24	23	47

Conclusions.—Treatment with 2400 r is often fatal to egg and polar nuclei. Many fruits in this class contained a large number of empty as well as filled seeds, indicating that often the integument alone had proceeded to final development. The empty seeds are frequently quite normal in appearance and difficult to distinguish from filled seeds. The integument thus appears more resistant to treatment by x-rays than the internal tissues of the ovule.

The crumpled appearance of the distorted empty seeds which occur in all classes might be taken as an indication of radiation damage to the integument rather than evidence of collapse of the internal tissues of the ovule. Yet empty seeds with the same degree of distortion are found when irradiated pollen is placed on the stigmas of untreated flowers. In this case the integument has not been treated and the subsequent distortion must be due primarily to collapse of internal ovular structure. The integument may suffer injury but it is difficult to distinguish between damaged and collapsed integument.

The ovary wall and placental column are more resistant to x-radiation than the other tissues of the ovary. The walls develop the texture, thickness, and shape of normal fruits and split at maturity even under large doses (pl. 11, fig. 4).

EFFECTS INDUCED WITH IRRADIATED POLLEN

Materials and Methods.—Mature pollen from shattered anthers of La Paloma flowers was gathered and placed in No. 2 gelatin capsules prior to radiation. The technical factors involved were the same as for the irradiation of ovaries. The capsules were held in place on the ring with small strips of Scotch tape. Following treatment the pollen was placed on the stigmatic surfaces of No. 6 flowers. Protection against undesirable pollination was provided. There were in all fourteen radiation classes. Beginning with 13,200 r and increasing at increments of 600 r, the treatments were carried on until a dosage of 18,000 r was reached. They were resumed at 20,000 r, and the following doses were given: 22,200, 23,400, 24,600 and 25,800 r. Eight to ten fruits were analyzed in each class.

Results: Classes 13,200 r to 17,400 r.—The seed set was abundant. In the classes through 16,800 the completely filled seeds exceeded the partially filled and empty seeds although this excess appeared to decrease as the dosage rose. There was a steady increase also in the number of ovules giving rise to flat, cup-shaped and distorted structures, indicating damage to male nuclei. In class 17,400 the filled seeds were about equal to the partially filled and empty seeds.

Class 18,000 r.—Seed was generally abundant, with filled seed equalling partially filled to empty seed in about half the fruits. In the remainder, the partially filled to empty seeds exceeded the filled. An increase in the number of flat, cup-shaped, and distorted structures arising from ovules activated to a somewhat lesser degree was apparent.

Class 20,000 r.—Filled seed appeared to be about equal to partially filled and empty seed. Large numbers of distorted ovular structures and ovules that had been merely activated were observed, indicating that an increasing number of ovules was receiving badly damaged male nuclei or was simply undergoing a purely chemical activation.

Classes 22,200 to 25,800 r.—In these groups there were fewer filled seeds than partially filled and empty seeds. The number of distorted ovular structures is far greater than the number of recognizable "seeds," whether empty or filled, indicating that most of the male nuclei have undergone damage (pl. 12, fig. 5).

The difficulty in measuring precisely the amount of damage sustained by the pollen grain is apparent in the following comparison. In class 23,400 r, nine fruits were analyzed. The average number of recognizable "seeds" (filled, partially filled, or empty) was 29 per capsule. The ratio of filled seeds to partially filled or empty seeds at one extreme was 1 to 9, at the other 0 to 50. The average was 1 to 36. Normal fruits of this size might contain from 100 to 250 viable seeds. The large number of ovules that had undergone stimulation but had failed to develop would therefore indicate a high degree of damage.

In class 25,800 r ten fruits were analyzed. The average number of recognizable seeds per capsule was 57.4, higher than in class 23,400, although again the number of ovules falling short of complete development is high when compared with the number of seeds occurring in a normal fruit. The ratio of filled to empty or partially empty seeds was 1 to 4.6. Although this is an extreme case, it illustrates the difficulty in giving a true evaluation of damage. Variation in the number of seeds, damaged or otherwise, or in the number of activated ovules, might be due in part to the number of pollen grains employed. However, it is more likely due to the degree of damage suffered by the pollen grain depending upon where and how it is hit.

In general, it seems safe to say that with increasing dosage, fewer filled seeds are developed, that the number of partially filled and empty seeds increases, and that finally the number of ovules merely undergoing some degree of activation increases. It would appear from examination of large numbers of activated ovules and completely hollow "seeds" composed only of integument that x-radiation of pollen grains, severe enough to kill nuclei, often does not nullify the stimulating effect of the activating substances or their precursors within the grains. The growth or activating components of the grains retain some ability to stimulate the ovary wall as well as the integument so that sometimes these fruits are of much the same size as a normal fruit (pl. 11, fig. 5).

The following tables indicate that no completely parthenocarpic fruits have been derived from x-rayed mature pollen, since even in the higher dosage classes, seeds capable of germination developed. Rick (1943), treating *Petunia* anthers immediately prior to anthesis, found that dosages as high as 50,000 r (200 KV, 10 ma, filters of ¼ mm. copper and ¼ mm. aluminum, target distance 10 cm., Wappler clinical unit) permitted the production of viable seed.

Germination test No. 1 was carried on under greenhouse conditions, the counts being made three weeks after sowing the seeds on moist filter-paper, following sterilization with Sarasan. Germination test No. 2 was carried on under the conditions described on page 103.

TABLE VI

GERMINATION TEST NO. 1 (Samples 100 seeds each)

Dosage r	Full germination to 2 cotyledons	Laggards	Total
Control	48	15	63
13,200	35	5	40
13,800	36	8	44
14,400	38	7	45
15,000	26	12	38
15,600	32	10	42
16,200	12	13	25
16,800	19	5	24
17,400	14	11	25
18,000	13	5	18
20,000	22	8	30
22,200	0	1	1
23,400	0	0	0
24,600	0	0	0
25,800	10	7	17

GERMINATION TEST NO. 2

Dosage r	Seed number per sample	Sample wt. (mg.)	Full germination to 2 cotyledons	Laggards	Total
13,200	100	7.20	21	10	31
13,800	100	7.03	20	20	40
14,400	100	8.44	19	16	35
15,000	100	7.00	20	18	38
15,600	99	8.24	20	15	35
16,200	100	7.04	6	6	12
16,800	100	6.64	19	7	26
17,400	100	7.29	4	12	16
18,000	100	5.83	9	4	13
20,000	100	6.40	11	5	16
22,200	100	4.65	2	1	3
23,400	55	2.23	0	0	0
24,600	55	1.85	0	0	0
25,800	100	5.41	6	2	8

PARTHENOCARPY INDUCED WITH POLLEN FROM X-RAYED ANTHERS

Since pollen grains collected at anthesis require such high dosages for inactivation, anthers were taken from La Paloma flowers about to open. At this time anthers contain pollen but are plump and juicy.

Materials and Methods.—The anthers were placed in a No. 2 capsule, irradiated, and then allowed to ripen and shatter within the capsule. The pollen was then applied to No. 6 flowers, with soda straws being used to prevent any additional pollination. The x-ray doses ranged from 5400 r to 13,800 r at increments of 1200 r. Only the most turgid anthers from a single flower were treated in each class because occasionally one anther may be non-functional.

Results.—Classes 5400 and 6600 r were the only ones in which any filled seeds were found (pl. 12, fig. 6). Variation in the effectiveness of radiation was apparent in these two groups; only one fruit in the "5400 r" class contained any filled seed while in all three of the "6600 r" group a few were found. No filled seeds were found in the remaining classes except in the "12,600 r" class where one fruit contained one filled seed. In general, it may be said that as the dosage increased, the number of empty seeds increased until the bulk of the ovules was merely in some stage of activation, some remaining completely unstimulated.

In the "12,600 r" class the ovary walls did not develop completely but remained papery at the base. The upper portions showed characteristic texture, thickness, and shape. These fruits were also the smallest obtained in addition to containing the least activated ovules. In this experiment there appears to be a decrease in the size of the fruit with increasing dosage, indicating injury to the pollen growth substances or their precursors.

None of the four flowers treated with 13,800 r pollen developed. This is not surprising in view of the effects of increasing dosage on fruit development. The fact that the flowers treated with pollen receiving a dosage of 10,200 r failed to develop either indicates variability in response or else that other factors were involved (pl. 11, fig. 6).

DISCUSSION

Murneek (1951) has concluded that synthetic growth substances are not in themselves always responsible for fruit development but rather that they stimulate in some fashion a hormone or hormones already present in female tissue. This view is not too far removed from that taken by many investigators with regard to the activity of pollen; that is to say, that the activity of pollen, aside from furnishing nuclei in the formation of embryo and endosperm, is based on a substance which sets into motion a hormone system resulting in ovary enlargement.

There are ample references to the hormone content of pollen grains in the literature of plant growth substances, and Muir (1951) sums up the situation when he states that pollen of all sorts probably contains auxin, but that it may vary in amount and in condition; auxin may exist in a free or bound condition or as a precursor, and failure to detect it has been due to faulty techniques. Wittwer (1951) contends, as has van Overbeek et al. (1941), that in an actual pollination the number of grains involved is too small to furnish adequate hormone material for fruit production. Muir's (1947) experiments are of particular interest here because of the relationship between *Nicotiana* and *Petunia.* Pollen of *N. Tabacum* was found to contain only small amounts of free hormone with somewhat larger quantities in the bound condition. The unpollinated pistil indicated no free hormone, but considerable hormone in the bound state. A water extract of pollen was found to release much larger quantities of bound hormone in the free condition from dried ovary tissue. In a later report (1951) he estimated

that following fertilization the auxin content in the ovary is 100 times greater than the maximum amount obtained from extraction of pollen. It was 30 times greater in the style. It would appear, then, that there is something in pollen other than its native hormone complement which instigates the release of hormones in the ovary following pollination. After fertilization the ovules become a rich source of hormones as indicated by the experiments of Wittwer (1943), Britten (1950), and others.

The development of integument and ovary wall need not in certain cases be dependent upon the development of endosperm and embryo. Studies with 2, 4-D and other substances have resulted in the production of parthenocarpic fruits filled with empty seeds. The use of foreign pollen, as shown here, occasionally results in parthenocarpic fruits containing empty seeds, the emptiness apparently due to genetic differences between sperm and egg, while the seed coat and ovary wall are stimulated by the less specific activators within the grain. Furthermore, pollen grains treated with x-ray dosages sufficient to render their nuclei genetically inactive, can still stimulate integument and wall growth although it has not been determined histologically as yet that fertilization followed by collapse of the system within the integument has not occurred. This last point deserves amplification. A glance at the data concerning the fruits produced with irradiated dry pollen shows that none of these was completely parthenocarpic. Even in the highest dosage class a few filled seeds developed and there were others partially filled. Since fertilized ovules are known to be rich sources of hormone, it is easy to visualize a diffusion of hormone material from fertilized to adjacent unfertilized ovules with the subsequent expansion of integument and wall tissues. Britten (1950), studying maize, concluded that naturally parthenocarpic fruits resulted from the activity of auxin products emanating from seeds developing close by. The spatial arrangement of parthenocarpic and normal fruits on the ear coincided with vascular supply. In these *Petunia* fruits, it would seem possible, even when male nuclei had been damaged, for fertilization to occur, and, providing that collapse of the fertilized egg apparatus did not take place too soon, a diffusion of hormones could begin. In the cases of parthenocarpic fruits produced by irradiating ovaries or turgid anthers, this does not appear to be as important a consideration, since the appearance of the integument indicates a very early collapse of the nucellus and they are usually completely empty. Radiation damage to the male nuclei had apparently been severe enough to prevent fertilization.

Whether integument can develop to any extent without development of the ovary wall remains to be seen. Some treatments in this study with 2, 4-D in lanolin at 1 p.p. 1,000 and at various concentrations in talc (when moisture was present) have resulted in small parthenocarpic fruits in which the only activated integuments were located on parts of the placental column opposite wall tissue showing normal thickening and texture. Those ovules opposite less-developed portions of the ovary wall such as the bases of these small fruits, which usually

remain thin and papery, showed little if any activity. To activate integument separately, an activator not stimulating other tissues would be necessary, and whether the space required for enlargement would be available without growth of the wall seems doubtful.

Since ovary walls and ovules can, under certain conditions, act independently, then 2, 4-D, when applied to the stigma of *Petunia,* is usually an activator for both systems. X-rayed pollen and the pollen of *Nicotiana affinis* would appear to be in the same category.

If we assume that it is possible for all pollen types to have within them certain activating substances in common but that the pollens of genetically related groups exhibit fewer and lesser differences among themselves, then it is possible to account for parthenocarpy arising as it does here from a combination of solanaceous pollen and *Petunia* stigmas. It is then possible to account also for the exceedingly mild activation provoked by the orchid pollen in *Petunia* ovaries. Such an explanation would require that basically similar pollen grains produce, or do not produce, results depending upon the orientation of these substances in a genetically suitable background. In short, they must find the proper kind of stigma. That nuclei involved in fertilization have a much stricter limitation placed upon them has been amply illustrated in the failures of numerous attempts to obtain seeds from certain interspecific or intergeneric crosses.

The activating substance or substances in pollen seems to be independent of the nucleus, in a functional sense at least, at the time of pollination, since parthenocarpic fruits tend to be produced by irradiated pollen although pollen nuclei have been damaged by x-rays. The substance appears to be more stable in the presence of x-rays than the nucleus. This stability is not as great when turgid anthers are irradiated as when dry pollen is treated as indicated by fruit size, and it is possible that such resistance varies with moisture content (Lea, 1947). The nuclei of dry pollen too require higher lethal doses than those in the moist anther, but here the question is further complicated in that the nuclei of dry grains are further removed in time from completion of meiosis than the nuclei of less mature grains.

SUMMARY

1. Fourteen types of pollen were placed on the stigmas of 349 *Petunia* flowers. Five of these pollen types were solanaceous, two of them (*Nicotiana affinis* and *Salpiglossis* sp.) producing parthenocarpic fruits which were somewhat smaller than normal fruits.

2. Parthenocarpic fruits have been produced in *Petunia* with 2, 4-D, x-rayed pollen, and x-rayed ovaries.

3. The effects of these methods are discussed with regard to fruit development.

4. The lethal dose for egg and accessory cells appears to be from 2400 to 3000 r under conditions outlined above. Completely lethal doses for nuclei of

moist pollen (in the anther) were about 6600 r and for dry pollen undetermined, but over 25,800 r. The ovary wall, the integument, and the placental tissue, perhaps because of their relative dryness, showed no ill effects from treatments up to 5400 r and responded normally to activating substances of pollen. The activator substances of pollen grains require a higher lethal dose than nuclei in both dry and moist pollen, although in treating moist pollen (in the turgid anther) these lethal doses are lower.

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Explanation of Plates

PLATE 11—FRUITS

Fig. 1. Control (left); *Cymbidium* male × *Petunia* female (note activation in upper half); normal *Petunia* fruit at right.

Fig. 2. Three parthenocarpic fruits from the cross *Nicotiana affinis* male × *Petunia* female. Normal *Petunia* fruit at right.

Fig. 3. Control; 2, 4-D in lanolin, 1 p.p. 1,000; 2, 4-D in lanolin 1 p.p. 100; normal.

Fig. 4. Six fruits from x-rayed ovaries treated with normal pollen. (2,400; 3,000; 3,600; 4,200; 4,800; 5,400 r). Normal fruit at right.

Fig. 5. Two fruits resulting from pollen treated with 25,800 r applied to normal flower. Normal fruit at right.

Fig. 6. Six fruits resulting from pollen treated before anthesis and applied to normal flowers. The largest fruit from each dosage class is shown here (5,400; 6,600; 7,800; 9,000; 11,400; 12,600 r). Normal fruit at right.

PLATE 12—SEEDS

Fig. 1. Normal seeds, × about 5.33.

Fig. 2. Hollow seeds of *Nicotiana affinis* male × *Petunia* female, × about 5.33.

Fig. 3. 2, 4-D in lanolin, 1 p.p. 100, × about 5.33. Some crushed seeds have been added to show the hollow condition.

Fig. 4. Hollow seeds from ovaries treated with 3600 r × normal pollen, × about 5.33.

Fig. 5. Seeds from pollen treated with 25,800 r × normal flowers, × about 5.33. Some crushed seeds have been added to show the hollow condition.

Fig. 6. Seeds from normal ovaries × pollen from anthers irradiated at 5,400 r prior to anthesis, × about 5.33.

1

4

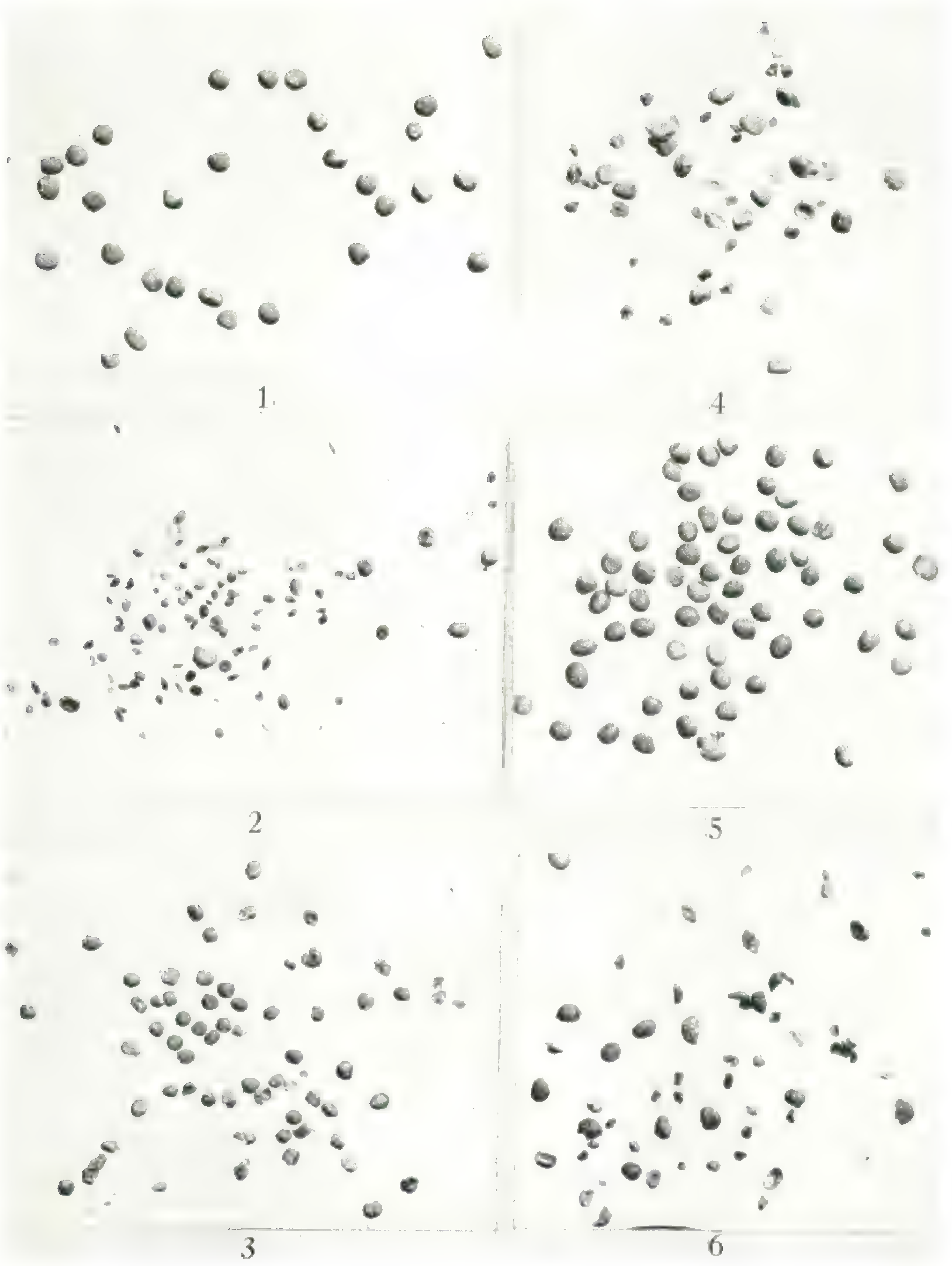
2

5

3

6

McQUADE—PARTHENOCARPY IN PETUNIA



McQUADE—PARTHENOCARPY IN PETUNIA

A GEOGRAPHY OF POKEWEED*

JONATHAN D. SAUER**

The plants we call weeds stand apart from their truly wild and truly tame fellows because of their special ability to establish themselves in artificial habitats. In spite of indifference or active repression by man, they have been able to thrive and multiply with the advance of civilization. By the very fact of their existence such plants suggest problems of special botanical and ethnological interest. There is the problem of the peculiar characteristics which have allowed the weeds to exploit disturbed places. There are also the questions of how the ancestors of modern weeds fitted into the ancient natural plant associations of pre-human times, how much these plants have evolved, and how far they have migrated since they first allied themselves with man.

General answers to such questions will require understanding of the stories of many individual species. Since only fragments of direct historical evidence on most weed species can be found in published records or herbarium collections, their stories must be reconstructed largely from indirect evidence. One of the most powerful lines of indirect evidence may be found in geographic distributions. The present geographic patterns of the weeds, like those of any phenomena irregularly distributed over the earth's surface, offer strong though sometimes complex and cryptic clues to their past stories.

This paper represents an attempt to describe and understand the distribution patterns of a single species, *Phytolacca americana* L. (= *P. decandra* L.; includes *P. rigida* Small), commonly called pokeweed or simply poke. Poke is in some ways an especially attractive subject for such a case study. The species is relatively clear-cut taxonomically and is the sole representative of its genus through almost its entire range. Thus a wealth of previous records can be used in studying its distribution, with slight danger of accepting mistaken identifications.

The gross range is considered first, followed by examination of the microdistribution. Finally, an effort is made to reconstruct some of the story of how poke became a successful weed.

Gross Range

NATIVE RANGE.—

Like most of the species of *Phytolacca*, poke is a native of the New World. Unlike all the other New World species, poke has its range centered north of the tropics. Its native area presumably includes a little of southeastern Canada, almost the entire eastern half of the United States, and a small area in the extreme northeast of Mexico. The northernmost outposts of a few tropical species reach into the Bahamas and northern Mexico. There they approach the southernmost

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University.

** Department of Botany, University of Wisconsin, Madison.

poke colonies of Florida and Texas; in northeastern Mexico there is some actual overlap of ranges. I have seen specimens of both typical *P. americana* and of tropical *Phytolacca* species which were collected at Monterrey in Nuevo León.[1]

The first available historical records of poke were made during colonial times in New England, Pennsylvania, and Virginia (Parkinson, 1640; Benson, 1937). Before 1850 poke was reported in Kansas (Townsend, 1839), close to its present western limit. Not until late in the nineteenth century are there enough historical records to give even a rough outline of the range of the species. By that time the increasingly adequate published floras and herbarium collections indicated a range approximating that of the present day, including such border-line areas as Ontario, Wisconsin, Minnesota, Iowa, Nebraska, Oklahoma, and Texas.

The available recent records of poke in eastern North America are mapped in fig. 1. The indicated locations are based partly on published local floras, too numerous to list here, partly on herbarium specimens I have examined, but mostly on private records and summaries of herbarium collections which were supplied by the botanists named in the acknowledgments. Special efforts were made to obtain adequate data from the states on the western and northern margins of the range, and the localization of dots within those states is probably significant. In the southeastern states the specific locations of the dots and their low densities probably signify nothing more than inadequate records. In spite of the scant records, there is reason to believe that poke is abundantly and generally distributed throughout the Southeast. In Arkansas, for example, "the plant is in every section of land in the state," according to Demaree,[2] while in Georgia poke has been seen in "more than 100 counties" by Cronquist.

At the present time poke seems to have a coherent distribution blanketing most of the eastern United States. Within the general limits of its range, large-scale gaps in the actual distribution may be found only in mountain areas. Toward the northern limit poke is reported only from very low elevations. As far south as New York State, it is infrequent at elevations above 1,000 feet. Figure 2 shows the available records of poke in New York, based mostly on unpublished data from the New York State Museum and the New York Botanical Garden, supplied by S. J. Smith. Contour lines are drawn according to Rafter (1905). In the more

[1] A few specimens of *Phytolacca* collected far to the south in Vera Cruz have been described by Walter (1909) as representing a variety of *P. americana*. Those specimens cited by Walter which are available to me resemble but are by no means identical with *P. americana* proper. The Vera Cruz colonies may be, as Walter assumed, simply aberrant and isolated tropical outposts of the species proper. However, they may be of hybrid origin. In key characters, including carpel and stamen number, *P. americana* is intermediate between certain tropical species which range into Vera Cruz. These species are known to hybridize elsewhere in tropical America, and some individual segregates from such crosses have the key characters of *P. americana* (Fassett and Sauer, 1950). I doubt if the taxonomic position of the specimens in question can be positively determined without much better samples of the *Phytolacca* populations of northeastern Mexico.

[2] Complete names and addresses of persons supplying unpublished data are given in the acknowledgments.

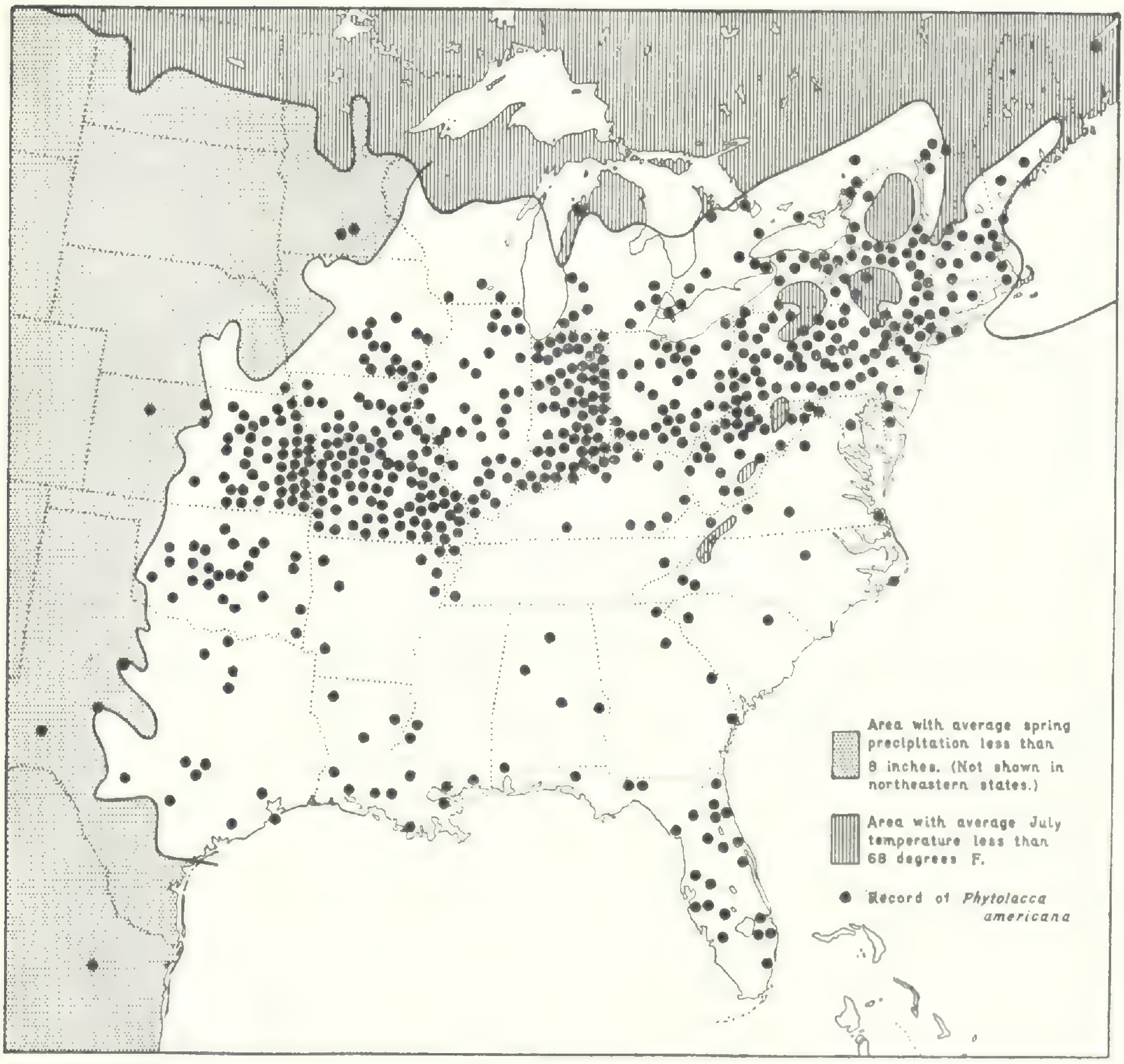


Fig. 1. Distribution of poke in eastern North America.

southern states poke may be absent only on the highest mountains; it has been found at elevations up to 2,000 feet in Pennsylvania, 2,500 feet in West Virginia, 4,000 feet in Virginia, 3,000 feet in Tennessee, and 2,800 feet in Arkansas.

The apparent absence of poke in some highland areas and the general east-west trend of the northern limit of the species suggest that its northward extent may be determined by temperature tolerances. Rough correlations can be made with various measures of temperature. For example, the plant has seldom been found in areas where the temperature falls below —20° F. in an average winter, so that winter-killing of the ordinarily perennial roots may sometimes be a limiting factor. However, the range can be correlated more closely with summer than with winter temperatures, and there is some experimental proof that summer temperatures are critical.

Lloyd (1914, 1917) planted *P. americana* seeds of unspecified origin at Carmel, California. He found that poke germinated and grew normally there, but pro-

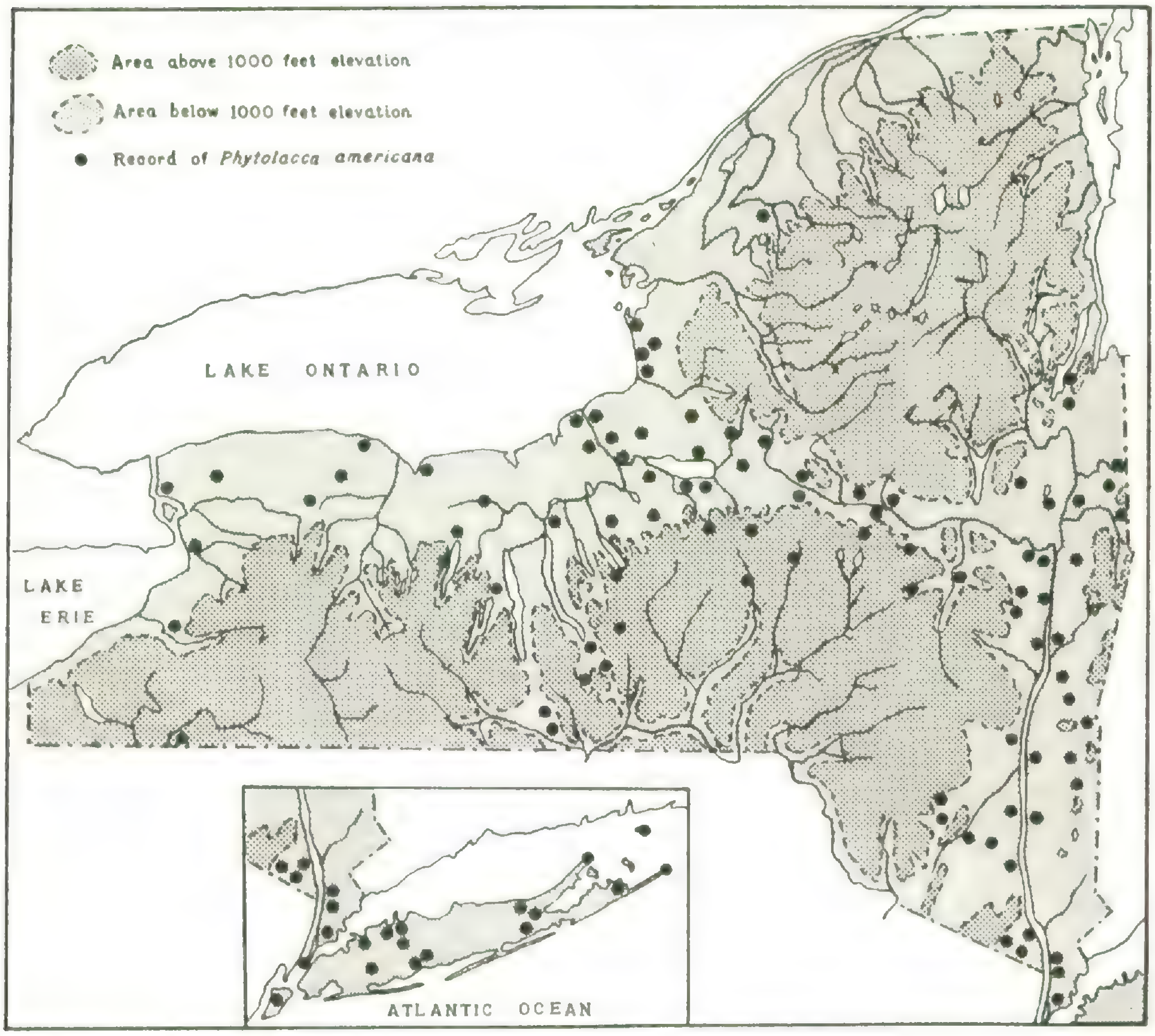


Fig. 2. Distribution of poke in New York State.

duced only abortive flowers when grown in the open. Plants exposed to slightly higher temperatures by being planted against a sunny wall, prostrated against the ground, or grown in an unheated, well-ventilated glass shelter, flowered normally and produced viable seed. Lloyd concluded that prevailing daytime temperatures at Carmel were about 5° F. below the critical level for seed production. During the period of his observations, the daytime temperature usually ranged between 60° and 70° F., exceeding 70° on less than a third of the days.

Although the precise limits of the northward extent of the species probably involve a complex balance of factors, it seems reasonable that the major control may be duration of temperatures above the minimum required for flowering and seed set. Since adequate temperature data in terms of durations are not available, a correlation can be attempted only with average temperatures. As shown in fig. 1, the line dividing zones with an average July temperature of over 68° F. from cooler zones approximates the northern boundary of the species fairly well.[3]

[3] All climatic data used in this paper are from Brooks and Ward (1936) and Kincer (1941).

The position of the 68° July isotherm in mountain areas also corresponds fairly well to the upper altitude limit of poke. In the New York area, this isotherm follows the 1,000-foot contour line, shown in fig. 2, rather closely, while farther south July temperatures average above 68° in all but the highest mountains.

The westward extent of poke appears to be limited by moisture rather than temperature. The western border, lying more or less along the 100th meridian in a zone of sharply decreasing precipitation, can be roughly correlated with various measures of moisture. Here again, the exact limitation of the range is probably controlled by a complex balance of factors, including water supply and transpiration rate during different stages in the life history of the plant. However, experience in growing poke plants indicates that moisture is most likely to be critical during the young seedling stage. Mature plants with their well-developed fleshy roots are much better able to stand drought. It seems reasonable that on the Great Plains border, rainfall during the seedling stage should be a major limiting factor. The line dividing zones with an average spring rainfall over 8 inches from drier zones approximates the western limit of the species fairly well, as shown in fig. 1. In the dry plains west of this line poke is very rare and is confined to peculiarly moist habitats, such as river bottoms. The plant becomes abundant in upland habitats only where spring rainfall exceeds 10 inches.

Thus it appears that, within its native area, the general distribution of poke is largely controlled by its climatic tolerances. Although poke has a long history of human use throughout this area (Sauer, 1950), man has ordinarily been satisfied with gathering the spontaneous supply of the plants. Deliberate propagation has certainly been attempted in isolated instances, but I know of no evidence that these efforts have in any way affected the gross range of poke in eastern North America.

AREAS OF RECENT INTRODUCTION.—

Outside its native area, poke owes a great deal of its distribution to human appreciation of its useful properties. Poke's most conspicuously successful colonization abroad is in the Mediterranean region, where it was introduced about 1650. Its berries proved so useful for coloring low-grade wines that the plant became widely cultivated in Portugal, Spain, France, and Italy (Ascherson and Graebner, 1915; Messedaglia, 1927). Escaping from cultivation, poke has become a fairly common weed in this region. It is reported from almost all the European and African countries bordering the Mediterranean Sea, and ranges northward into Switzerland, southern Germany, Austria, Hungary, and Russia, eastward to Persia, and westward to the Azores, Canaries, and Cape Verdes (Walter, 1909; Hegi, ca. 1910; Ascherson and Graebner, 1915; also specimens in the Missouri Botanical Garden Herbarium). Poke has occasionally been planted as an ornamental in some European countries, including England and France (Saint-Hilaire, 1809; Weathers, 1901). A form with variegated foliage, propagated by root division, was once sold commercially in Paris (Carrière, 1887).

The violent drug properties of poke seem to have had little to do with its propagation in Europe. It is mentioned in very few of the European books on medicinal plants. However, introduction of the species elsewhere may be traceable to its drug effects. Poke is reported to have been brought to Cuba as a cultivated medicinal plant (Roig y Mesa, 1945). Introduced into South Africa, poke has naturalized itself as a weed around settlements; the juice of the berries is used for coloring food and beverages, while the roots are used as medicine by the Kaffirs (Marloth, 1913; Watt and Breyer-Brandwijk, 1943). The species is also reported as an adventitious plant in such widely scattered areas as California, Arizona, Bermuda, Asia, Australia, and Macronesia, but no details are available (Walter, 1909; Ascherson and Graebner, 1915; Britton, 1918; Robbins, 1940; Kearney and Peebles, 1942).

Micro-distribution

A brief inspection of records of occurrence of the species or a casual look at the plants in nature shows immediately that poke has a peculiarly spotty distribution pattern throughout its range. The poke population, even near the heart of its native area, is made up of solitary individuals and scattered colonies, all closely associated with disturbed habitats. Thus poke presents a curious picture of a plant which behaves like an immigrant weed, even in its homeland, and seems to occupy a niche in no natural plant association.

FIELD STUDY OF MICRO-DISTRIBUTION.—

In an effort to understand the peculiar distribution pattern of poke, a small area in the heart of the native range of the species was selected for detailed field study. The sample area, shown in fig. 3, is part of the Missouri Botanical Garden Arboretum at Gray Summit, 35 miles west of St. Louis. It covers a narrow strip about one mile long, running from the alluvial Meramec River bottoms up over rocky bluffs with limestone outcrops, to a rolling upland capped with silt loam. The vegetation cover is highly varied, including cultivated fields, pasture, former farmyards, natural glades, and woodlands of many different ages and compositions, but with oaks, maples, and hickories predominating. All the poke plants that could be found in this area in the early fall of 1947 are mapped on fig. 3.

Upland colonies.—About forty plants were growing along a dry gully in the northwest corner of the area. Most of these were mature plants, scattered through the brush on the gully sides; some young seedlings had come up where brush had been recently cut. In the open grassland at the very head of this channel, there was a small group of seedlings where the turf had been cut by running water. There were several more upland colonies near the road in the north-central part of the area. Most of these plants were either actually on the sites of former farm buildings or close by in an old mule yard, kitchen garden, and similar areas of once intensive human activity. According to the records these buildings were torn down at different times between 1938 and 1942. For the last few years the

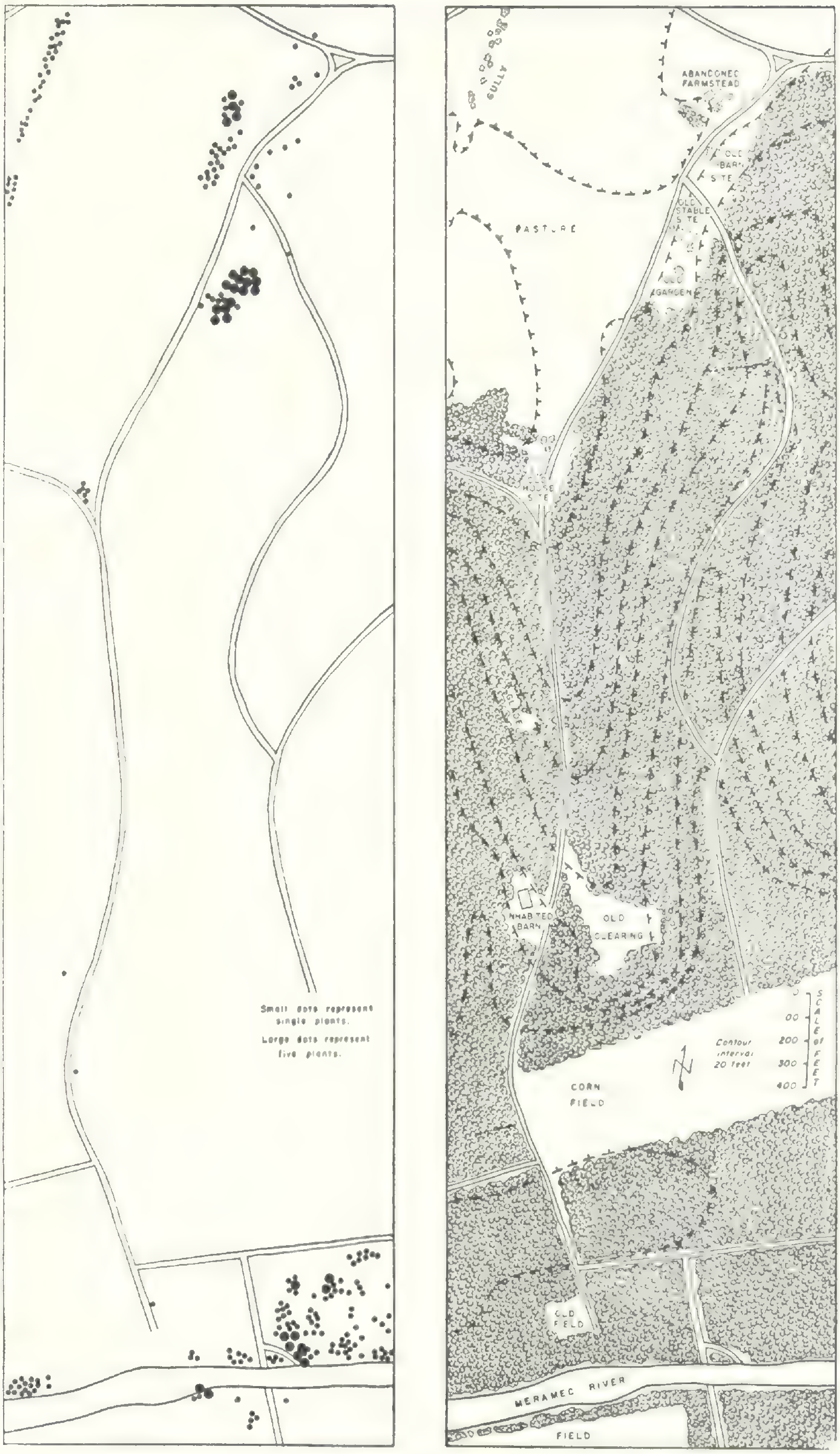


Fig. 3. Distribution of poke in area of field study.

area had been lightly pastured and mowed almost every summer, and at the time of mapping was covered with a heavy bluegrass sod. No seedlings were found in the unbroken grassy sod. Most of the poke plants were quite old and appeared to be hanging on from past periods of disturbance. From each of the tremendous, profusely branched perennial roots, sometimes over a foot in diameter, grew large numbers of short slender stems. Leaves and inflorescences were relatively small.

Numerous seedlings surrounded a newly fallen tree at the south end of the old kitchen garden and were scattered over a fresh excavation near the old farmhouse site at the north end of the area. A single seedling was coming up in the fresh gravel of a road behind the old stable site. These younger plants had only one or two stems from each slender root; their stems, leaves, and inflorescences were relatively large.

Except for two solitary and unhealthy looking individuals, no poke was found between the old upland farm sites and the river bottoms.

River-bottom colonies.—There had been some recent human activity in the river bottoms also. The south bank had been partially logged two years previously; on the north bank small-scale timber cutting and gravel digging were in progress during the year of mapping. Flourishing poke colonies were crowded around brush piles and felled trees in these disturbed places.

Many other river-bottom colonies, including abundant seedlings, occupied sites where there was no trace of human activity. They were scattered through the more open river-bank woods, most often among sycamores, but sometimes among hackberry, soft maple, cottonwood, or elm trees. All of these colonies occupied places where there was very little low-growing vegetation. No poke was found in mature woods where there was a heavy growth of other herbs or in cut-over areas with a dense stand of brush or young second-growth timber.

Although there was no sign that man had ever disturbed many of the river-bottom sites occupied by poke colonies, another factor causes repeated and violent disturbance of this habitat. During an average spring or early summer, the Meramec leaves its banks at least once. The poke colonies lie in the zone of maximum flood frequency. Piles of river drift, beds of fresh sand and other alluvium, caving banks, and raw cuts give good evidence of the powerful disruption effected by the river. Roots of some of the old poke plants had been almost completely exposed; these plants were stunted, sometimes dying, although many were still able to bloom and fruit. Where roots were covered by fresh alluvium, sometimes as much as two feet deep, the plants were flourishing. Among these were found the largest plants in the area mapped, some measuring 12 feet from root crown to branch tip, bearing enormous leaves, some of which approached two feet in length. The stout, sparsely-branched tap-roots plunged straight downward into the sandy soil for more feet than I cared to dig.

The colonies three years later.—In the summer of 1950, I revisited the same area to look for any changes in the poke population. The gully in the northwestern corner of the area had been filled in by bulldozers and was heavily trampled

by cattle coming to drink at a newly constructed pond. The poke colonies in that part of the area were completely obliterated. Along the road on the other side of the same pasture, about a dozen plants remained of the more than fifty which had been present in 1947. The poke plants, though seldom eaten by cattle except when very young, had suffered from the increased cow traffic around the new pond. The site of the largest colony had been scuffed completely bare, and some of the survivors in other places had recently been stepped on and broken. Half a dozen new seedlings were found in this part of the area, a few under trees and bushes, a few in the open by a new excavation.

The fenced pasture extended only to the road, and the area east of the road had not been regularly grazed. The single plant on the trail behind the old stable site was gone, as were all but five of the twenty plants around the fallen tree. However, all the other plants present in 1947 to the east of the road seemed to be still present and healthy and a few new ones had come up here and there. The biggest outburst, including about twenty new seedlings, was on a pile of orchid peat dumped the year before near the old stable site.

Down the hill, the solitary individual in the woods near the barn was gone. The other poke plant at the corner of the cornfield was still alive and still alone.

In the river bottom, the colony at the western edge of the area seemed to be about the same size as before, although the plants were immersed in a dense mass of other herbs which had come in since 1947. The colony of a dozen plants on the south edge of the river had been carried away, along with many tons of river bank, by stream cutting. The habitat of the other river-bottom colonies remained essentially as before—open woods with some minor new cutting and filling. The previous mapping had not been sufficiently precise to permit spotting many of the former plants as individuals, but the population of mature plants as a whole had held its own and a moderate number of new seedlings were scattered through this part of the river bottom.

OTHER HABITAT RECORDS.—

The diverse habitats occupied by poke in the area of field study, including both damp river-bottom woods and well-drained open uplands, appear to be characteristic of the species over most of its range. Habitat notes in published floras and on herbarium specimens indicate that poke is able to tolerate a remarkable variety of temperature, light, and moisture conditions. Its micro-distribution appears to be limited by climatic conditions only near the northern and western margins of its range. Moreover, soil texture and acidity do not appear to be the usual limiting factors. Poke is common in clayey as well as sandy soils and tolerates a wide range of pH (Palmer and Steyermark, 1935; Deam, 1940).

The only factor common to all the reported habitats is the ever-recurring theme of disturbance of the soil and of the plant cover. A canvass of habitat notes from all available sources shows that two classes of sites are repeatedly mentioned from all parts of the range. One group of notations involves sites dis-

rupted by man's activities: old orchards, gardens, old pastures, hog-yards, neglected barn-yards, dumps, clearings, burns, and habitation sites. The other group of notations indicates no artificial disturbance but mentions places where stream erosion and deposition would be expected: ravines, river banks, low woods near creek, river-bottom woods, woods flooded in spring, alluvial woods, low ground.

It should be mentioned in passing that association with disturbed habitats is not peculiar in the genus *Phytolacca* to *P. americana*. The weedy behavior of two tropical American species of *Phytolacca* and their hybrids has already been described from Fassett's field observations in Colombia (Fassett and Sauer, 1950). The fragmentary available information indicates that most other members of the genus are characteristically weedy also.

SEED DISPERSAL AND VIABILITY.—

The association of poke and disturbed ground is most intimate and most apparent in the case of seedling plants. Old well-established poke plants can hang on for at least a few years in the face of considerable competition from other herbs; quite early in the season they are able to produce vigorous leafy shoots from their great perennial roots. Seedlings start growth later in the spring and develop relatively slowly. Where they must compete on an equal footing with other herbs, poke seedlings appear to be at an almost hopeless disadvantage. One of my experimental field plantings, given only an initial cultivation, was almost completely killed out by heavy growth of amaranths and other weeds which came up after the poke seedlings were well started.

In order to exploit the shifting and temporary spots of bare soil where they are free from choking competition, these plants require an efficient seed dispersal mechanism. Poke is poorly equipped for dispersal by wind or water. The mature fruits, with the seeds embedded in the slowly drying berry, remain firmly attached to the inflorescence even as the stalk dies. Dispersal ordinarily occurs only if the fruit is picked and transported by some animal. Birds are without doubt the usual dispersers of poke seed, as is suggested by the close association of poke with bushes and fences as well as by the sudden outbursts of isolated new colonies. It is well known that birds eat pokeberries frequently and regularly; at times the berries form one of the chief foods of the smaller migratory birds (Shultz, 1795; Grieve, 1931; Parks, letter).

The rapidity with which quantities of poke seedlings spring up in freshly disturbed sites, far from any former colonies, suggests the possibility that disturbance sets off germination of dormant seed. Poke seeds are viable for an extremely long time. Seeds buried in 1902 at depths too great for germination gave 80 to 90 per cent germination upon being unearthed in 1941 (Toole, 1946). Their long life would allow poke seeds to accumulate in the soil from occasional bird droppings over a long period of years until some disruption provided conditions suitable for germination.

Conclusion

The distribution patterns of poke suggest possible answers to the questions of what peculiar characteristics have enabled poke to exploit disturbed places, what habitats it occupied in pre-human times, and how the species has been affected by its life with man.

In spite of being weak in competition and poorly equipped to spread by methodical progressive advance, this plant has some special characteristics which have made it a successful weed. One of these is its relatively broad tolerance of light, microclimate, and soil conditions. Equally important are the production of berries attractive to birds and the long life of the seeds. Wide bird dispersal and high seed viability, even after many years of dormancy, give poke a head start over its competitors in the race to colonize isolated spots of newly opened ground. Given sufficient head start, mature poke plants, with their great perennial roots, can survive among more competitive but later arriving herbs for enough years to produce their contribution of seed.

The micro-distribution patterns of poke provide what seems to be a significant clue to the ancient habitat of the plant: Everywhere, even in the heart of its native range, poke is bound to disturbed sites and nowhere does it seem to belong to a stable plant association. Poke seedlings appear to be able to establish themselves only where some external factor has intervened to obliterate the potential competitors and open up a patch of raw soil. Before the coming of man, poke could have found a niche in habitats disrupted by natural agencies. Its stronghold may have been in open stream-bank woods, where new ground was constantly opened by cutting and filling. Poke undoubtedly colonized other natural scars in the mantle of vegetation—gullies, landslides, burns, blowdowns—but away from the constant intervention of the stream such colonies could ordinarily persist only briefly until they were overwhelmed by the slow advance of more aggressive vegetation.

With the invasion of North America by man, the area of ground bared to poke colonization must have increased, slightly at first with the earliest primitives, considerably more as Indian agriculture spread, and enormously since the European settlement. In its native area, the general range of the species appears to be climatically controlled and may have been changed very little by human activity. Certainly, there is no evidence of migration by the plant in this region in historic times. Within the old limits, poke colonies must have multiplied and spread in artificial habitats until today the colonies occupying naturally disrupted sites form a minor and easily overlooked part of the greatly expanded population.

Outside its native area, the general range of poke has been greatly extended by man in the last few centuries. Because of its useful properties the plant was deliberately introduced into other continents, where it has naturalized itself as a minor weed.

With the great expansion of the poke population in artificial habitats, new strains especially adapted to the new conditions might have been expected to evolve. So far as I can judge, there is no evidence that such evolution has taken place. The poke of natural river-banks and forest blowdowns and the weed of settlement margins and abandoned fields are morphologically indistinguishable. Poke's success as a weed of the cultural landscape appears to be based, not on evolution during human times, but on its previous adaptation as a pioneer species of naturally disturbed places. The story of poke is thus of a different nature than the stories of those weeds, including many tropical *Phytolacca* populations, which are the product of recent hybridization and selective modification in artificial habitats.

Acknowledgments

I am indebted to Edgar Anderson, of the Missouri Botanical Garden, for suggesting this investigation and for guidance throughout its course. I am also indebted to the following persons for communications containing original observations and data from herbarium collections: the late W. A. Anderson, State University of Iowa; Lillian Arnold, Florida Agricultural Experiment Station; E. Lucy Braun, University of Cincinnati; Clair Brown, Louisiana State University; Eva Butler, Groton, Connecticut; Earl Core, West Virginia University; V. L. Cory, Southern Methodist University; Arthur Cronquist, Washington State College; Delzie Demaree, Arkansas State College; Norman C. Fassett, University of Wisconsin; John M. Fogg, University of Pennsylvania; George J. Goodman, University of Oklahoma; the late Ada Hayden, Iowa State College; G. N. Jones, University of Illinois; Rogers McVaugh, University of Michigan; H. B. Parks, Agricultural and Mechanical College of Texas; Harold A. Senn, Central Experimental Farm, Canada Department of Agriculture; Aaron J. Sharp, University of Tennessee; Lloyd Shinners, Southern Methodist University; Stanley Jay Smith, New York State Museum; Julian A. Steyermark, Chicago Natural History Museum; B. C. Tharp, University of Texas; and the late C. A. Weatherby, Gray Herbarium of Harvard University.

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THE GAMETOPHYTE OF *CARDIOCARPUS SPINATUS* GRAHAM

HENRY N. ANDREWS* AND CHARLES J. FELIX**

Among the more interesting fossils that we have encountered in coal balls from West Mineral, Kansas (Andrews, 1951), is a seed, presumably of cordaitean affinities, with a rather well-preserved gametophyte. It seems to be referable to *Cardiocarpus spinatus* Graham (1935, p. 165), although it presents much additional information relative to the structure of the integument and gametophyte. The final selection of a name for the seed presented a considerable problem, and because of some general principles of seed nomenclature, it seems desirable to discuss in detail certain historical aspects of the case.

In 1828 Brongniart recorded (Prodrome, p. 87) the genus *Cardiocarpon* and listed five species. The only description given is as follows: "Fruits comprimés, lenticulaires, cordiformes ou réniformes, terminés par une pointe peu aiguë." Brongniart did not deal with the genus in his monumental 'Histoire des Végétaux Fossiles' (1828–1838) and seems to have had little or nothing to do with it until 1881 when his work on the silicified seeds appeared. Various other authors, however, have described species of *Cardiocarpon,* some soon after 1828, and the variation in form illustrated composes a rather incredible array of what are apparently many generic entities. A few examples will suffice to reveal the lack of recognition of any clearly defined generic boundary. Mantell (1844, p. 153, fig. 34-1) figures under the name *Cardiocarpon acutum* a round strongly winged seed; the wing apparently entirely encloses the body of the seed. Lindley and Hutton (1831–37, pl. 76) illustrate wingless seed casts under the same name. Dawson (1878, fig. 194b) pictures a seed with a strongly attenuate apex under the same binomial; and Williamson (1877, pl. 15, fig. 122) figures a bicornute seed under the name "*Cardiocarpon acutum* of Lindley and Hutton," although the binomial was originally Brongniart's (1828, p. 87). In 1853 Newberry described *Cardiocarpon samaraeforme* as a nearly round seed with two large and distinct wings; while Dawson's figures show *Cardiocarpon cornutum* as an elongate winged seed with cornute apex.

The above is a very brief introduction into the almost endless range of form of the seeds gathered together under this generic designation. More fuel was added to the flame of confusion when in 1862 Geinitz created the genus *Cordaicarpon,* the generic description differing in no significant way from that of Brongniart's for *Cardiocarpon.* Geinitz (1855) described *Carpolithes cordai* (which he believed to be the seed of *Cordaites principalis* (Germar) Geinitz) and designated it (in 1862) as the type species of his new genus. In referring to his illustrations (Geinitz, 1855, pl. 21, figs. 7–16), we find it impossible to recognize any characters which set his genus apart from Brongniart's or in any way justify a distinct genus. To further confound later workers these generic names, originally given as

* John Simon Guggenheim Memorial Foundation Fellow at Harvard University, 1951.
** Graduate Assistant, Henry Shaw School of Botany, Washington University, St. Louis.

Cardiocarpon Brongniart and *Cordaicarpon* Geinitz, have since been variously cited as *Cardiocarpus* or *Cardiocarpum* and *Cordaicarpus* respectively.

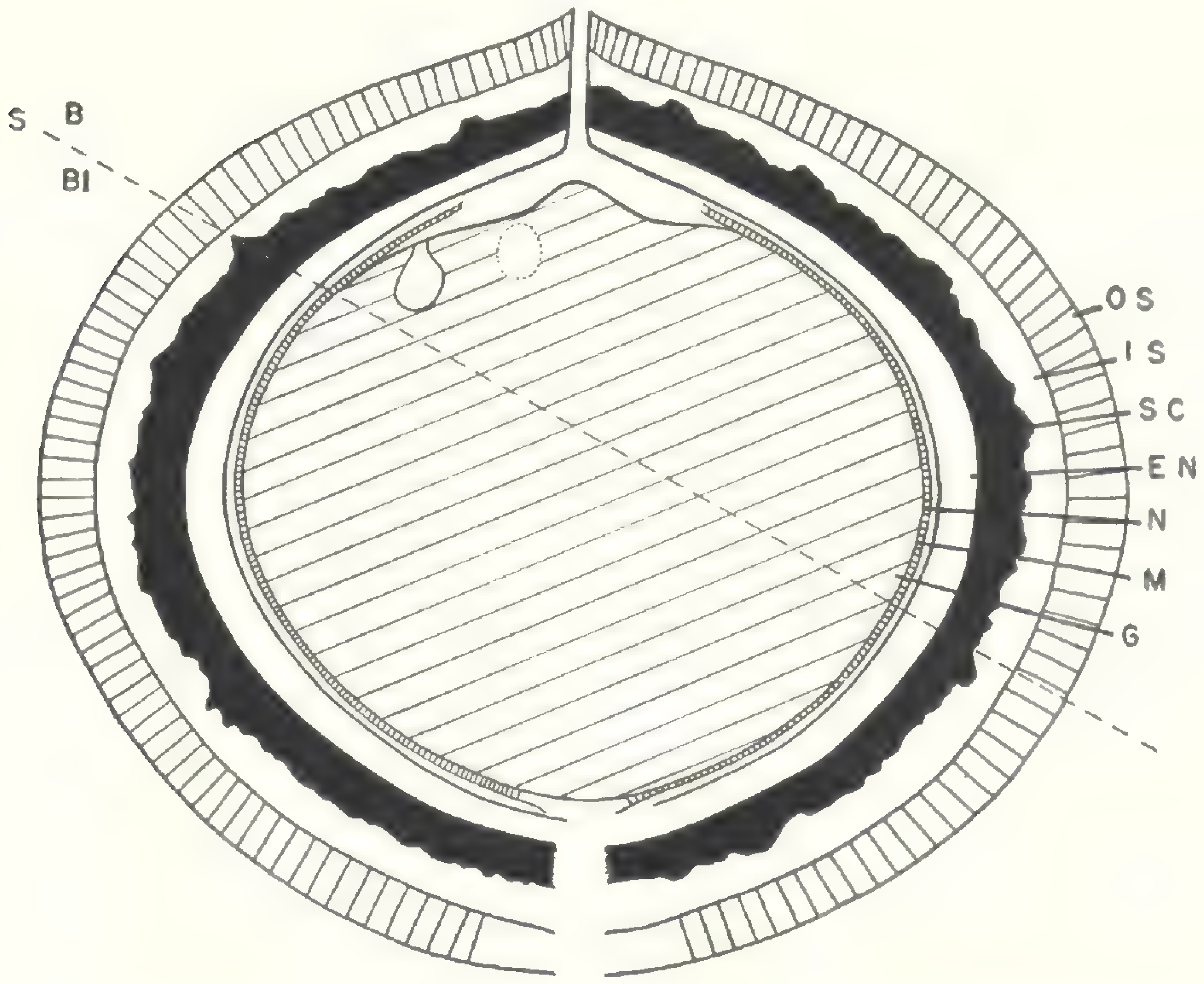
The next, and indeed significant, phase in the history of these fossils was Brongniart's description in 1881 of petrified seeds which he assigned to *Cardiocarpus*, thus emending the original generic concept (of *Cardiocarpon*) to include structurally preserved remains.

In an effort to alleviate the chaotic state in which these two genera existed, Seward (1917, p. 338) proposed that *Cardiocarpus* be restricted "to petrified seeds exhibiting the characters described by Brongniart" in 1881, and that *Cordaicarpus* should serve "for platyspermic seeds, preserved as casts or impressions, having a comparatively narrow border enclosing an ovate or cordate-ovate nucule; the base is either rounded or cordate" (p. 354). Since the spellings employed by Seward have been used by most workers for several decades, it seems to be most expedient to continue them.

Seward's usage of these two generic names was intended to be useful, and his desire to create a workable basis for dealing with such fossils is commendable. However, a system of classification based on mode of preservation is apt to run into difficulties sooner or later, the introduction of better techniques and discovery of intermediate types of preservation presenting notable obstacles to such a system. Thus, a complicating but interesting link was presented by Miss Reed (1946) when she described certain compression fossils preserved in shaly limestone from Iowa in which a considerable amount of cellular detail is recognizable. She has provisionally referred these specimens to "*Cardiocarpon affinis* Lesquereux." Further consideration of this fossil will be taken up below.

We may next consider *Cardiocarpus spinatus*, a seed described by Graham (1935) from an Illinois coal ball. Judging from the description, his specimens were very poorly preserved; his accompanying figures show no cellular detail. Apparently, the distinctive feature of the seed lies in the spiny nature of the sclerotesta. Darrah (1940) refers to this fossil under the name *Cordaicarpus spinatus*. It is not clear why he uses Geinitz' genus *Cordaicarpus* which was based on impression specimens and which Seward (1917, p. 354) proposed to continue in use as a genus in which casts and impressions would be relegated. It seems evident that Darrah had better-preserved material available, although his description is brief and the single illustration (fig. 22) given is at too low a magnification to be informative.

We now return to the fossils in our own collections which we believe are referable to *Cardiocarpus spinatus* Graham and which contribute further to our knowledge of the structure of this seed. This description is based on two coal-ball specimens from the Fleming coal which occurs in the upper part of the Cherokee shale, Des Moines series, middle Pennsylvanian, about four miles south of West Mineral, Kansas. One specimen (No. 783) contains a well-preserved gametophyte and the other (No. 721) is significant for the preservation of the integument.

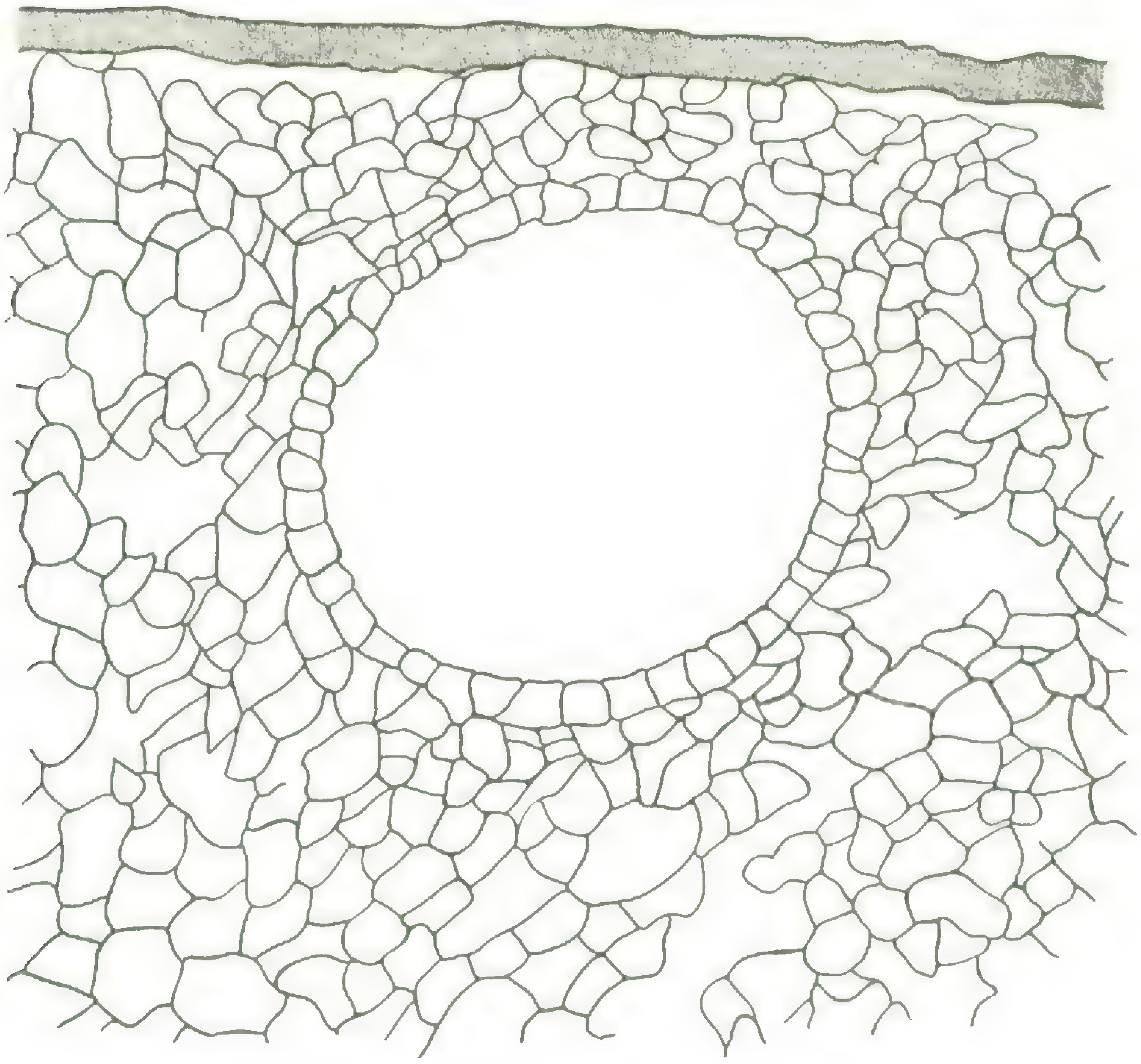


Text-fig. 1. *Cardiocarpus spinatus*, a diagrammatic longitudinal section: G, gametophyte; M, megaspore membrane; N, nucellus; EN, endotesta; SC, sclerotesta; IS, inner sarcotesta; OS, outer sarcotesta.

The initial saw-cut of No. 783 which exposed the seed was made at an angle of approximately 30° to transverse as is indicated by the dotted line "S" in text-fig. 1. Two series of peels were started from the respective surfaces, one going toward either end, although at the initiation of these series it was not possible to be sure of the exact orientation of the seed. Thus a series of peels was started in the "B" direction which are labelled 783-B-S1, etc., and a series in the B1 direction which are labelled 783-B1-S1, etc. When at peel B-S 4 a structure appeared which gave evidence of being an archegonium and was confirmed in the following peels, it was evident that the "A" direction was the micropylar one. A total of 48 peels was made in this direction although the apex of the gametophyte was passed at B-S36. A series of 30 peels was made toward the chalazal end labelled B1-S1 to B1-S30, at which point a tangential series was started parallel to the broad lateral face, these being labelled B1-S'1, etc.

It may be noted that all measurements given below are corrected to account for the 30° divergence of these peels from the true transverse.

In a median section the seed containing the gametophyte measures 11.0 × 7.5 mm. The following tissues may be noted (text-fig. 1; pls. 13 and 14, figs. 1, 4, 5), starting from the inside: *G*, gametophyte; *M*, megaspore membrane; *N*, nucellus; and the integument consisting of: *EN*, endotesta, the cellular structure of which is very poorly preserved; *SC*, sclerotesta, the conspicuous portion of the integument characterized by its spiny outgrowths (the walls of this tissue are



Text-fig. 2. *Cardiocarpus spinatus.* Enlarged view of an archegonium as shown in the upper part of fig. 2, pl. 13. A few of the jacket cells have been restored. Stipple band indicates megaspore membrane.

somewhat thicker than those of the cells composing the sarcotesta outside but not as markedly so as might be assumed from a casual observation[1]); and finally the thick fleshy sarcotesta which is composed of two strikingly different tissues (figs. 4, 5)—an inner region, *IS*, which extends hardly beyond the outer limits of the spines of the sclerotesta, and an outer region, *OS*, which is distinguished by much larger cells. In fig. 1 only the inner sarcotesta is preserved.

While studying a coal ball (No. 721) containing a medullosan stem from the same locality we encountered another seed in which an undoubted complete sequence could be observed from sclerotesta to epidermis (figs. 4–6). Here it may be noted that the cells of the inner sarcotesta are small (averaging about 55 μ in diameter) when compared with those of the outer sarcotesta which are about three times as large. The latter are delimited by a clearly defined epidermis (fig. 6). The extreme rarity of this outermost tissue in the fossils is understandable in view of the relatively large size of the cells and their thin walls; judging from its thickness (about 1 mm.) in the one specimen we have in which it is well preserved, this would give a revised statement of the diameter of the seed as 13.0 $\times$ 9.5 mm. instead of the 11.0 $\times$ 7.5 cited above.

[1] In most specimens it is only the sclerotesta that is preserved. We are inclined to believe that the durability of this tissue is to be attributed in part to the preservative quality of the cell contents as well as to the slightly thicker walls.

The gametophyte.—

As far as its gross cellular organization is concerned, the gametophyte is almost entirely intact. The intercellular substance appears to have decayed so that the cells have the appearance of being loosely held together although there is no appreciable distortion. The cell walls are clearly defined when observed by reflected light, yet the little organic matter remaining renders the walls so very light in color that it is not possible to obtain satisfactory photographs.

The gametophyte measures approximately 8.7 $\times$ 4.0 mm. in transverse section and about 7.5 mm. in length. It is ovoid except for the apex which appears to display the usual "tent pole" form. The latter is evident in oblique section in peel B-S35.

Two archegonia are present in the gametophyte. As indicated above, one begins to appear in B-S4, attains its maximum diameter of 0.5 mm. at about B-S10, and at S18 it appears to open out. The second archegonium appears between peels B-S23 and B-S32. Both of the archegonia are on one side of the seed, one being somewhat above the other. Little else can be said other than the fact that these organs are delimited from the rest of the gametophyte by a jacket of conspicuously smaller cells (text-fig. 2).

Other Carboniferous female gametophytes.—

Several examples of well-preserved gametophytes are now known from the Pennsylvanian, the lycopods being most abundantly represented. Scott (1901) described the gametophyte of *Lepidocarpon lomaxi* and *L. wildianum*, and more recently Andrews and Pannell (1942) described the gametophyte of the American *L. magnificum*. Schopf (1941) has given a good account of the gametophyte of *Mazocarpon oedipternum*, and Darrah (1938) has recorded a *Selaginella* gametophyte with exceptionally striking nuclear details. Other fossil lycopod gametophytes have been described by McLean (1912) and Gordon (1910).

Referring to the Carboniferous seed plants proper, Brongniart (1881) has figured gametophytic tissue in several seeds from St. Etienne in the genera *Cardiocarpus*, *Leptocaryon*, *Rhabdocarpus*, *Taxospermum*, and *Stephanospermum*. Although his beautifully executed illustrations show what is apparently the gametophyte, and in several instances the position of the archegonia and egg cells, clearly defined cellular details are not given. More recently Long (1944) has described the gametophyte of *Lagenostoma ovoides* in an excellent state of preservation.

Taxonomic considerations.—

There seems to be no doubt that the specimens of *Cardiocarpus spinatus*, originally described by Graham (1935) and later by Darrah (1940), are specifically identical with those described here. In view of the fact that our specimens add appreciably to our knowledge of the seed an emended description is given below.

It seems important also to comment on the semi-petrified seeds described by Miss Reed (1946) as *Cardiocarpon affinis* Lesquereux. Her contribution is interesting and significant, particularly from the standpoint of correlating impression or compression fossils with typically petrified ones, and it clearly points out the difficulty of retaining without revision Seward's classification of these seeds. There is, moreover, little doubt in our minds that the coal-ball seeds of *Cardiocarpus spinatus* are specifically identical with Reed's specimens. The problem therefore lies in specifically correlating all of these with Lesquereux's specimens, first described by him as *Cardiocarpon affine* (1860, p. 311) and later as *Cardiocarpus affinis* (1880, p. 564), the latter spelling being the acceptable one in our opinion. In an attempt to settle the problem we have examined Lesquereux's type specimen which is preserved as No. 8038, Paleobotanical Collections, Botanical Museum, Harvard University, and we have illustrated it in fig. 3. It is hardly more than an impression, there being but little organic matter present. It conforms very closely in size and shape with our coal ball specimens, but it displays no evidence of the spiny sclerotesta which is the most distinctive feature of the seed. It is of course possible that decay took place before a durable impression of this tissue could be left in the matrix. However, lacking this evidence we do not feel that there is adequate justification for including any of the other specimens mentioned above under Lesquereux's binomial.

Cardiocarpus spinatus Graham, emend Andrews & Felix.—

Platyspermic seeds with integument consisting of endotesta, strongly spinose sclerotesta, and sarcotesta, the latter being composed of two distinct zones; cells of the outer sarcotesta about three times as large (diameter) as those of the inner sarcotesta; seeds approximately 13.0 $\times$ 9.5 mm. in diameter, and containing a gametophyte bearing two archegonia.

Origin of specimens.—

Graham, 1935: McLeansboro group, Pennsylvanian; Calhoun coal mine, Richland County, Illinois.

Darrah, 1940: Des Moines series, Pennsylvanian; Shuler and Urbandale coal mines, Waukee, Iowa.

Andrews and Felix: Cherokee shale, Des Moines series, Pennsylvanian; four miles south of West Mineral, Kansas.

Acknowledgment.—

The senior author wishes to express his sincere appreciation for aid received from the John Simon Guggenheim Memorial Foundation and for the facilities placed at his disposal by the Botanical Museum, Harvard University.

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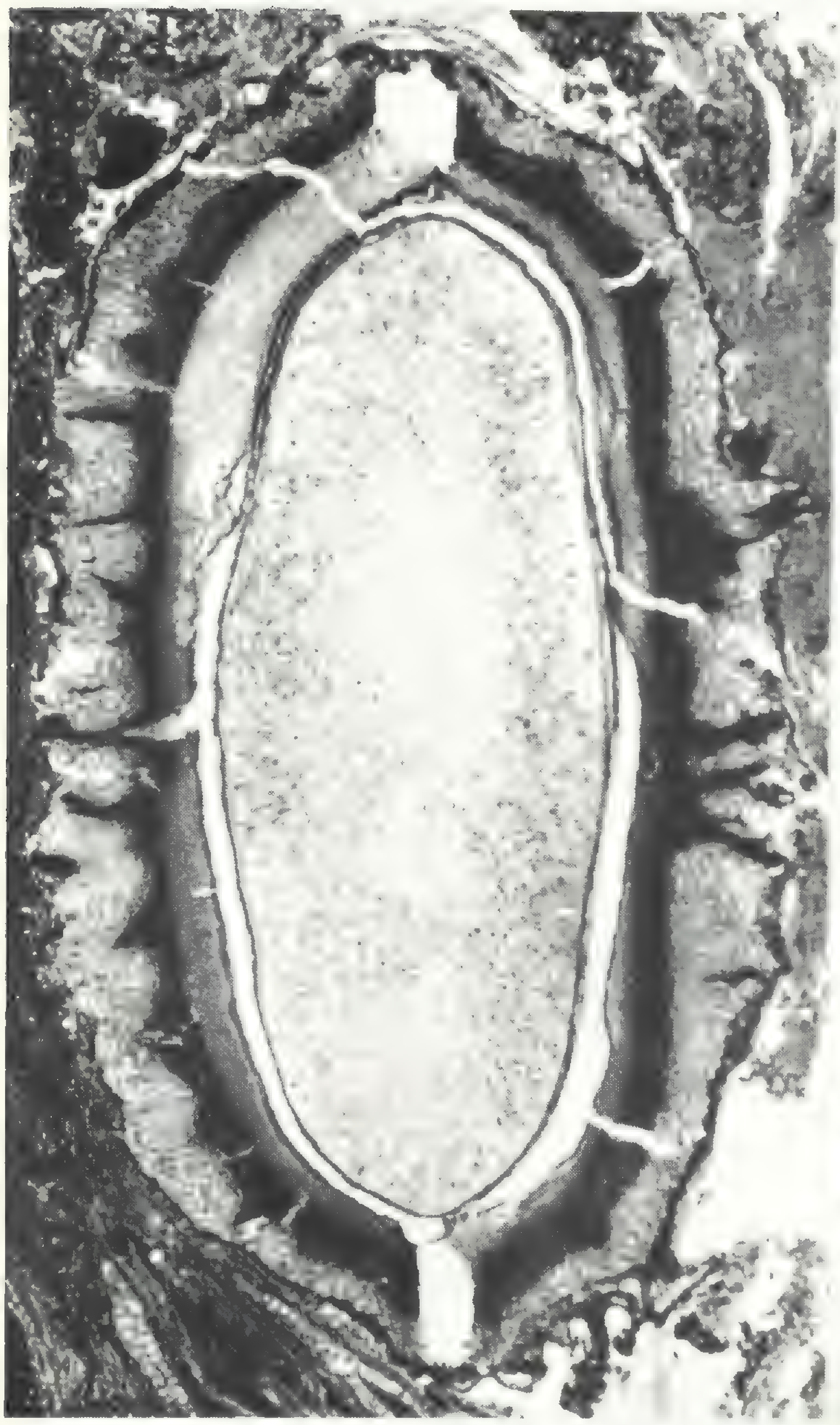
Explanation of Plate

PLATE 13

Cardiocarpus spinatus Graham

Fig. 1. A nearly transverse section through a seed containing a gametophyte. Actual plane of the section is indicated by dotted line "S" in text-fig. 1. The outer sarcotesta is not preserved in this specimen. Peel 783-B1-S18.

Fig. 2. Enlarged view of the gametophyte showing an archegonium in the upper part of the figure. Peel 783-B-S13.



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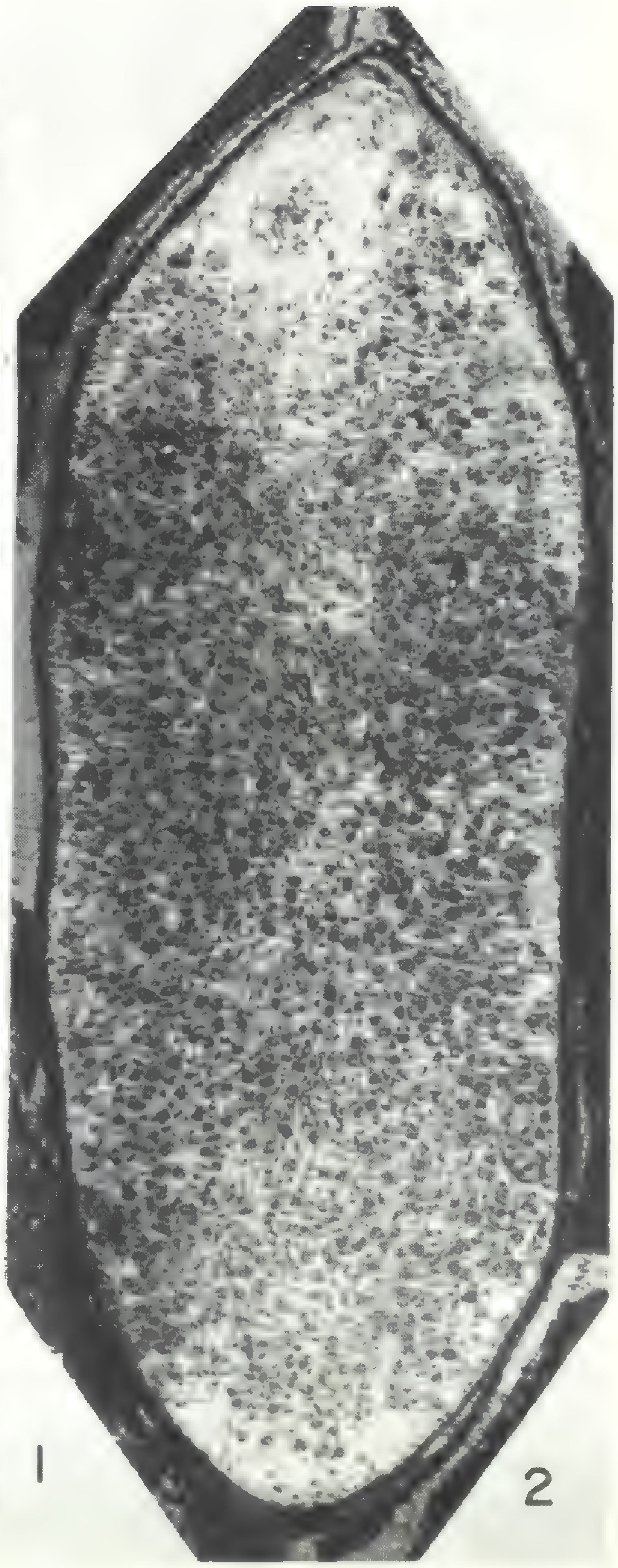

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ANDREWS & FELIX—*CARDIOCARPUS SPINATUS*

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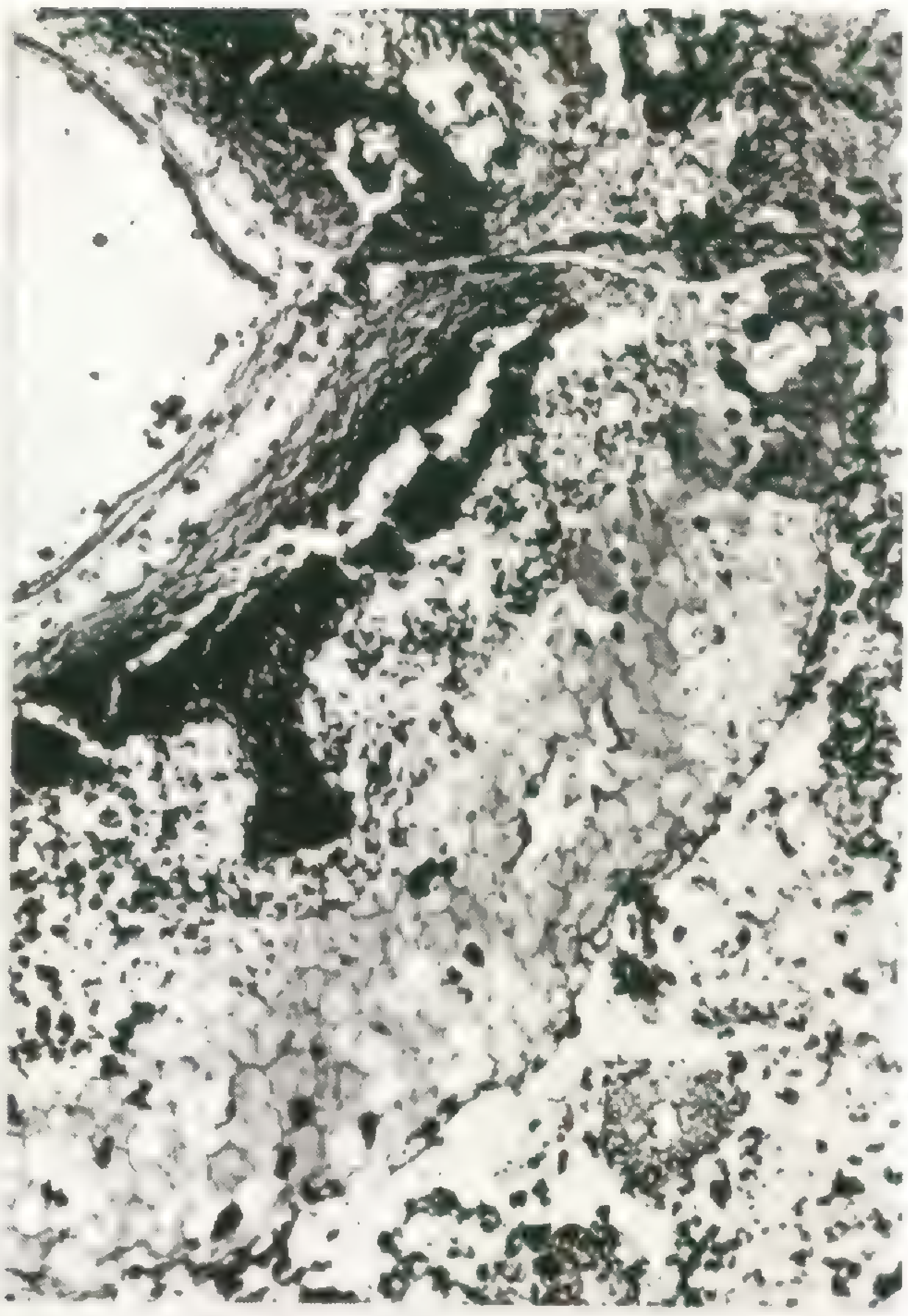

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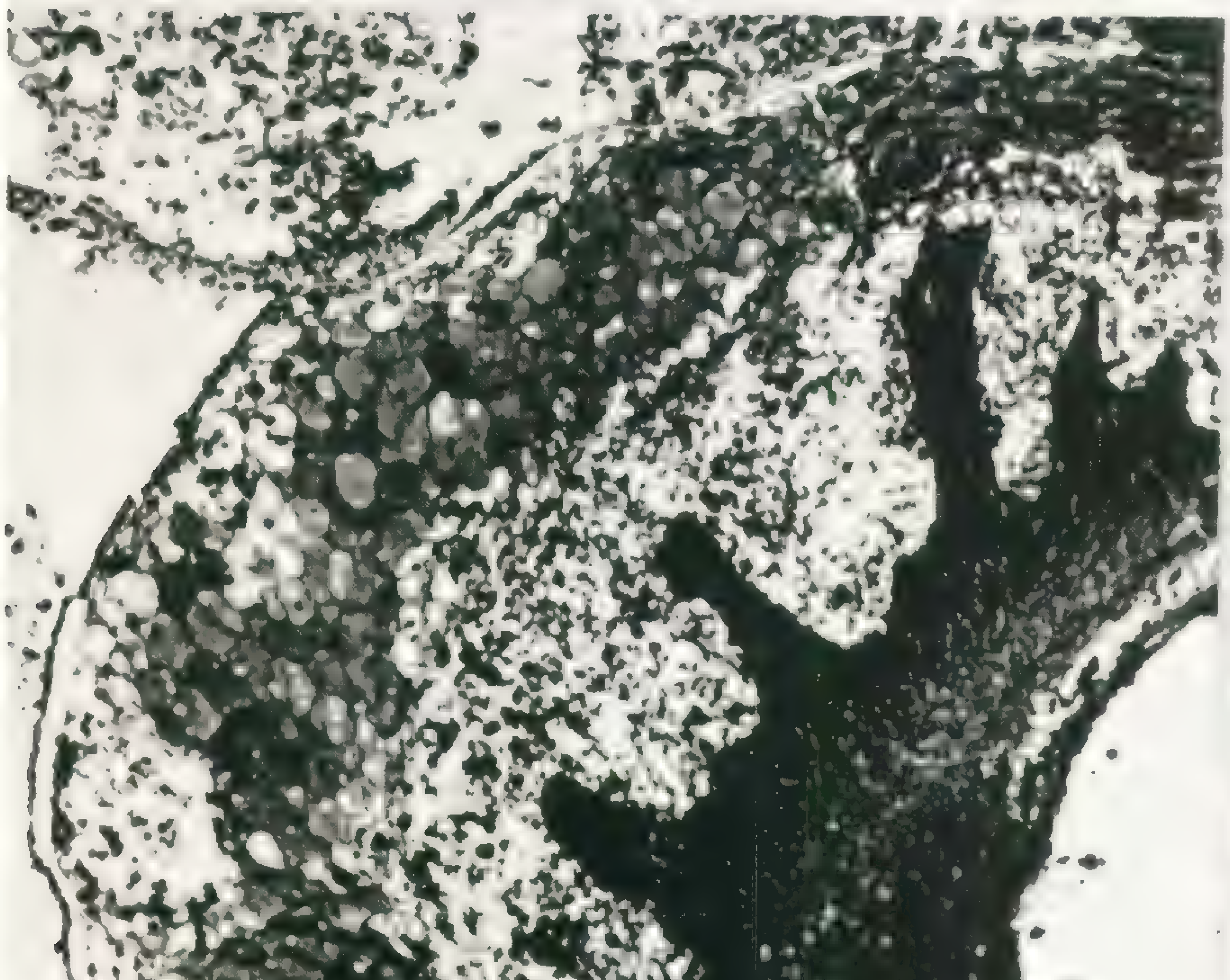

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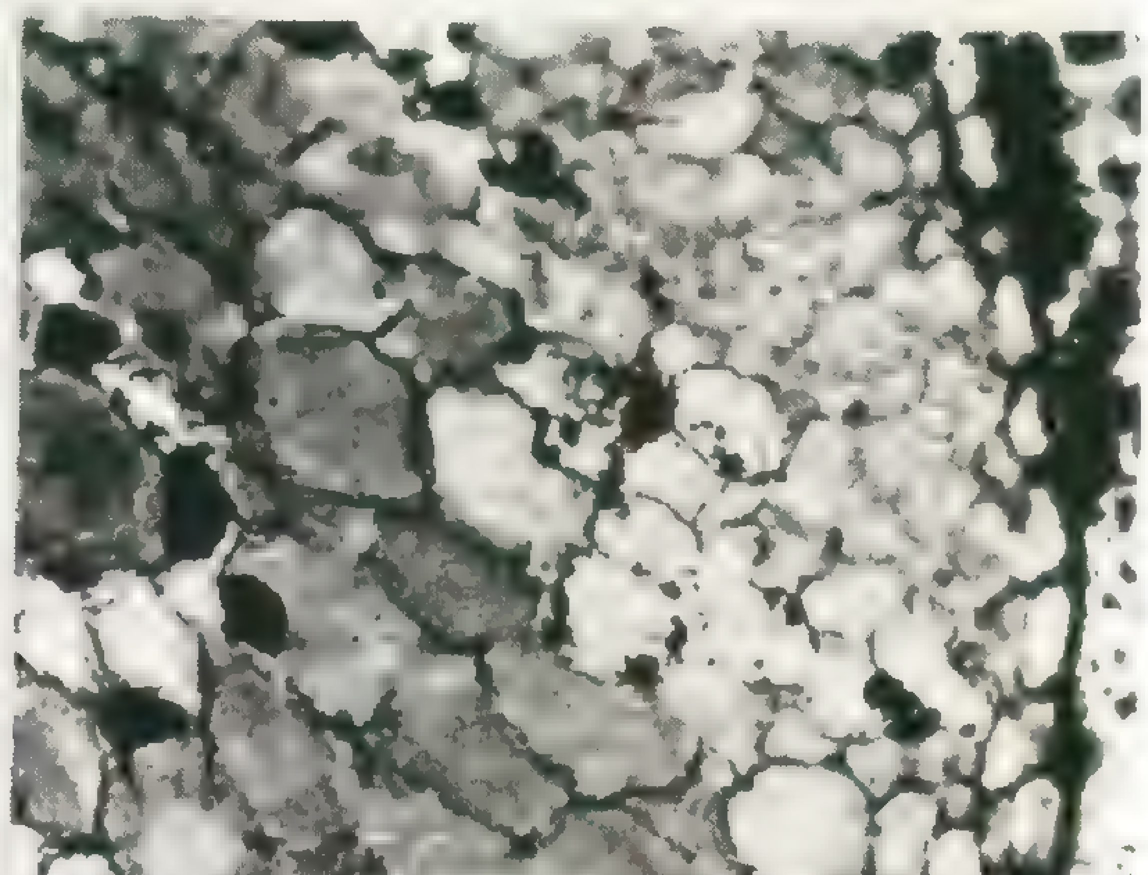

ANDREWS & FELIX—*CARDIOCARPUS SPINATUS*

Explanation of Plate

PLATE 14

Fig. 3. *Cardiocarpus affinis* Lesquereux. Photograph of the type specimen, No. 8038, Paleobotanical collections, Botanical Museum, Harvard University. × 12.

Cardiocarpus spinatus Graham

Figs. 4, 5. Transverse sections of the seed showing well-preserved outer sarcotesta. Slide No. 1967. × 19.

Fig. 6. The outer sarcotesta and epidermis enlarged. Slide No. 1967. × 54.

FACTORS AFFECTING THE MORPHOLOGY OF *CANDIDA ALBICANS**

DAN OTHO McCLARY**

Introduction

Most morphological studies on the yeast-like fungi have been conducted on natural substances—malt extract, corn meal, and various vegetable decoctions such as potato and carrot, as broth or solidified with agar. Since growth on these chemically unknown substances yields a great variety of morphologically different forms, there is much controversy as to their true morphologies and the causes for their variations. For this particular group of fungi and perhaps for others which are somewhat more stable morphologically, more precise physiological information seems to be needed than can be obtained on natural media in order to arrive at definite conclusions concerning morphological variation. It is the purpose of this study to define the morphology of a well-known species grown in media of known chemical composition under carefully controlled physical condition, in the belief that much of the existing confusion in the taxonomy of this group of fungi can be eliminated by use of such an approach. *Candida albicans* was chosen because of its extreme variations in form, and because of the extensive studies which have been made upon it.

I am indebted to Dr. Carroll W. Dodge for suggesting this problem and for his generous help throughout the course of the study.

Classification.—Although the yeast-like organism described by Robin in 1847 as the cause of the disease known in modern literature as thrush, muguet, sapinho, and Soor has been known for over a hundred years, there is apparently little agreement among mycologists as to its taxonomic position or even its name. Robin (1853) first named the organism *Oidium albicans.* Quinquaud (1868), realizing that the organism did not belong in *Oidium,* placed it in his new genus, *Syringospora,* naming it *Syringospora Robinii.* He not only described the characteristic clusters of blastospores, but he also presented drawings definite enough for one to be reasonably certain that he referred to the organism now known as *Candida albicans* (Dodge, 1935; Skinner, 1947). In 1877 Grawitz called attention to the differences between the yeast form and the mycelial form. He also described chlamydospores and even discussed the action of the media on morphology; but it is thought that he may have been working with mixed cultures because of his crude culture techniques. He believed this organism to be the same as *Mycoderma vini.* Reess, in 1877, showed that the organism was distinct from *Mycoderma vini* and called it *Saccharomyces albicans.* Plaut, in 1885, was the first to apply modern cultural technique. He identified the mycelial form with *Monilia candida* Bonorden on decaying wood. Stumpf, in 1885, concluded that he had two organisms, one

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the degree of Doctor of Philosophy.

** Assistant Professor of Microbiology, Southern Illinois University, Carbondale, Ill.

filamentous and one yeast, both liquefying gelatin. In 1885 Baginsky studied the organism on various media, and Klemperer produced experimental mycosis from intravenous injections.

Audrey (1887) first proved the connection between yeast and mycelial forms, showing that yeast cells were more common on solid media, filaments in liquid. Roux and Linossier (1890) studied the physiology in considerable detail, giving extensive notes on carbon and nitrogen metabolism without definitely describing the biochemical reactions. They describe their organism as producing white, elevated, creamy colonies, with surface slightly furrowed on cooked carrot. At first the yeast cells predominate, then there are some filaments for a short period, and finally yeast cells again. On liquid media the filamentous forms predominate except in malt extract. On most fruits (except melon) and on peptone gelatin, the yeast form is abundant. On sucrose gelatin both forms are found. No ascospores were observed, but chlamydospores were not uncommon on most media used.

In 1923 Berkhout introduced the new genus, *Candida*, and designated *Monilia candida* Bonorden 1851 as the type species based on a culture isolated by Kloecker under the name *Monilia candida* but "evidently not that species" (Dodge, 1935). To avoid the use of a repeating binomial, Berkhout changed the name to *Candida vulgaris*.

In 1934 Diddens and Lodder adopted Berkhout's genus, *Candida*, but they designated another species, *Candida albicans*, as the type. This name has persisted in spite of the objections of most of the other well-known mycologists including Dodge (1935), Conant (1940), Mackinnon and Artagaveytia-Allende (1945), and Skinner (1947). All agree that it should be *Syringospora* Quinquad 1868 by right of priority. This organism appears in the literature under a number of other names, but most of the important work concerning it may be found under *Monilia*, *Syringospora*, and *Candida*. The organism used in this study was received from the American Type Culture Collection as *Candida albicans*, and that name will be used in this paper.

General Morphology.—There are many morphological descriptions of this highly pleomorphic organism in the literature (Quinquaud, 1868; Grawitz, 1877; Audrey, 1887; and many others). The close correlation between the physiology and morphology of this organism is generally recognized, so that culture conditions and the medium used are always given with the morphological description. Skinner's description (1947) is a generally accepted one:

> Except for the chlamydospores there is little other morphological detail that will set a strain of *C. albicans* apart from the other species. Freshly isolated cultures show little tendency to formation of true or pseudomycelium unless grown in starvation media below the surface, as in scratch corn meal agar plates or potato infusion broth, or in sugar-free beef peptone gelatin stabs. Grown on ordinary Sabouraud agar the cells are almost exclusively of the budding yeast type. Strands of mycelium may penetrate into the substrate after prolonged incubation, but they are much more numerous and appear more promptly along the scratch in corn meal agar. Blastospores are invariably produced from the strands, but the arrangement of blastospores varies so much between isolates that discussion of this

has little value in a review of this sort. They tend to occur in ball-like clusters in fresh isolates, but not to the extent that they do in *Candida albicans* var. *stellatoidea.*

Morphological variation.—Morphological variations described in the literature are of two distinct types:

1. Irreversible changes called "degeneration" (a seemingly gradual change) and "dissociation" (a sudden but irreversible change) involving a mutation.
2. Reversible changes depending entirely on environmental conditions.

Irreversible changes.—This type of variation has been studied by Negroni (1935), Mackinnon (1940), Mickle and Jones (1939), Cavallero (1939), Martin and Jones (1940), and Conant (1940). Mackinnon (1940) described "membranous variants" and "lethal variants." In the "membranous variants" the blastospores become elongated into filaments, causing a characteristic wrinkled, or in more advanced variants, a spiky hard colony surrounded by a filamentous halo. In liquid medium this variant produces a mucous veil and the virulence diminishes. The biochemical properties do not suffer qualitative changes. The "lethal variation" is characterized by a lower rate of growth, a great diminution or total loss of virulence, and by increasing difficulty to produce mycelial growth. These variations may occur spontaneously as described by Mackinnon, or they may be induced by toxic substances such as immune serum (Negroni, 1935) or by lithium chloride and immune serum (Mickle and Jones, 1939).

Although the existence of these "dissociations" are accepted by most mycologists, Langeron and Guerra (1939) concluded, after their investigations of these "irreversible variations" made over a period of some ten years, that the S (smooth phase) is the normal one and the R (rough phase) develops as a result of various factors, chief of which are the reaction (pH) of the medium and "elongation factors" (presence of carbon dioxide, nutrients of a high molecular weight, and nitrates). These variations were reversed when the organism was transferred to fresh media. They did not find irreversible variations as reported by Mackinnon and others.

Reversible changes.—It is with this type of variation which occurs promptly when the organism is transferred from one set of culture conditions to another that this study is primarily concerned. In 1930 Talice published perhaps the most complete study and review of the factors influencing the reversible changes in this organism. He determined that production of filaments depends upon partial anaerobiosis, weak concentrations of nutrients in the culture medium, the strain of the organism used, the treatment it has undergone, and the age of the culture. He believed that the filamentous form is always the young form; the yeast form is the old form.

In 1938 Langeron and Guerra found the formation of filaments to be stimulated by prolonged culture in the laboratory, presence of high concentrations of carbon dioxide, and changes in the constituents of the medium during the course of growth, particularly the change in pH. Morquer and Nystérakis (1948) reported that certain concentrations of heteroaxine (beta-indole-acetic acid) stimulate filament formation.

Nickerson and Jillson (1948) found that a metabolic product of *Trichophyton rubrum* would inhibit the filamentous phase of *Candida albicans* but had no effect on the yeast phase. They considered that a separate enzyme system controlled each of these two phases and that the morphology of any given culture depended upon a stimulation or suppression of one or the other of these two systems which are supposedly competing for the same substrate. Nickerson (1950) again attributed the morphology of the yeast-like fungi to a delicate balance between growth and cell division. If the balance were upset in such a manner as to permit only growth to occur, elongated cells without cross walls would be formed. Cell division is, according to him, associated with the maintenance of intracellular sulfhydril (-SH) groupings. In slide cultures of *Candida albicans* grown on a synthetic medium consisting of glucose, ammonium sulfate, inorganic salts, and biotin, Nickerson found only the yeast form. When commercial or purified starch was substituted for the glucose, abundant filamentation and chlamydospores were produced. By adding cysteine to the medium, filamentation and chlamydospore formation were prevented and only yeast cells were formed. He concluded there must be a certain amount of a readily assimilable carbohydrate such as glucose in order to maintain the high oxidation-reduction potential essential for the intracellular -SH groupings required for proper cell division.

In general, one must conclude from the findings in the literature that where conditions are favorable for rapid multiplication, as with easily assimilable carbohydrates and with abundant aeration, the unicellular yeast forms predominate. Reduced oxygen tension, starvation media, liquid media in general, high pH, high temperature, or practically any condition or set of conditions which inhibits growth but does not stop it entirely, tend to produce the mycelial growth of *Candida albicans.*

General physiological characteristics.—In practically every taxonomic work dealing with this organism, its ability to produce acid and gas from various carbohydrates has been used. Most workers agree that the organism produces both acid and gas from glucose, fructose, mannose, and maltose; acid and sometimes gas from galactose; and acid but never gas from sucrose. Kluyver and Custers (1940) and van Niel and Cohen (1942) have published papers concerning the biochemistry of carbohydrate fermentation of the yeast-like organisms. According to van Niel and Cohen, there is no essential difference between the fermentation of glucose and sucrose by *Candida albicans* except that it occurs at a considerably faster rate in glucose.

In addition to carbohydrate fermentation tests, most authors also include a study of various nitrogen compounds as possible sources of assimilable nitrogen for the organism. Most of this work has generally been on synthetic media consisting of a sugar for a carbon source and inorganic salts (auxanograph). Wickerham (1946) showed that certain nitrogenous compounds which have been reported as unassimilable are readily used if the proper growth factor or

factors is present in sufficient quantity in the auxanograph medium. Burkholder (1943), using chemically defined media, found that biotin is required for the growth of *Candida albicans* and that thiamin is stimulating. The work of Morquer and Nystérakis and of Nickerson and his co-workers was done largely upon chemically defined media. However, except for the substitution of starch for sugar by Nickerson in one of his media, their work consisted of studying the various substances which are supposed to have certain physiological effects on cell elongation or cell division. There has apparently been no attempt to determine the effects of altering various other essential components of the medium.

Methods

The organism used for the greater part of this study was obtained from the American Type Culture Collection as *Candida albicans 2091*. Five other cultures were sent by Dr. J. E. Mackinnon at the request of Dr. Carroll W. Dodge. These organisms were maintained on media consisting of: glucose, 1 per cent; Difco yeast extract, .5 per cent; and agar, 2 per cent.

Culture media.—The medium used, essentially that described by Olson and Johnson (1949) and hence to be referred to as "basal medium," is as follows:

Sucrose	10.0 gm.	Calcium pantothenate	1.0 mg.
Potassium chloride	1.0 gm.	Inositol	5.0 mg.
KH_2PO_4	0.2 gm.	Thiamine-HCl	200.0 microgm.
$MgSO_4.7\ H_2O$	10.0 mg.	Pyridoxine	200.0 microgm.
Amm. citrate (dibasic)	6.0 gm.	Zinc sulfate	400.0 microgm.
Calcium chloride	50.0 mg.	Ferric ammonium	250.0 microgm.
L-asparagine	2.0 gm.	Copper sulfate	25.0 microgm.
Biotin	2.5 microgm.	Bacto agar	20.0 gm.
Riboflavin	75.0 microgm.	Distilled water to	1000.0 ml.

To facilitate the preparation of the several media required, stock solutions of vitamins and trace elements were prepared, preserved with toluene, and stored in the refrigerator.

In addition to variations of the above medium, various natural media with modifications as indicated were used. These include Bacto yeast extract, Bacto peptone, Bacto malt extract, corn steepwater, Bacto beef, Bacto corn-meal agar, and potato and carrot decoctions. Various sugars (C.P.) and other chemicals were used as indicated.

Although most mycologists insist that morphological studies should be made *in situ* as cover-glass or slide cultures or that the cultures be examined directly on the petri plate (Skinner, 1947), this method has been used to only a limited extent in this study. Almost all this work was carried out on agar slants or broth cultures in test-tubes. This method was believed necessary for at least four reasons: (1) With the many hundreds of cultures used in such a study, so much time would be consumed in making microcultures that they could not very well be continuously observed. (2) Slide and petri-dish cultures, when subjected to prolonged examination, become much more easily contaminated. (3) It was found that, probably due to the rapid exhaustion of nutrient material, slide cultures did

not undergo all the changes which were observed on slants. (4) A macroscopic as well as a microscopic examination was desired for each culture. Petri-dish and cover-glass cultures were, therefore, used only to verify observations made on slant cultures.

Slides for microscopic examination were made by transferring a bit of material from the slant to a slide upon which had been previously placed a drop of water or staining solution. A nichrome wire hook bent at a right angle about ⅜ inch from the end was used rather than a loop because the cultures were, under certain conditions, so tough that they resisted any amount of pressure that could be applied to them with a loop. Acetocarmine was found to give excellent results, the organism staining a bright red against a relatively colorless background. Since this stain evaporates quite rapidly, it was necessary to seal the preparation soon after the cover slip was in place. Turtox slide-ringing cement obtained from the General Biological Supply House, Inc., Chicago, Illinois, was found to be very satisfactory for sealing.

Verification of the Species

For morphological verification, agar slants of basal medium, .5 per cent yeast extract, and .5 per cent malt extract were inoculated with *C. albicans* A.T.C.C. 2091 and incubated at room temperature (25–30° C.).

For biochemical verification two types of media were used: (1) .3 per cent peptone, 10 per cent gelatine in distilled water for gelatine liquefaction tests; and (2) a series of nine carbohydrate media consisting of .3 per cent peptone with brom thymol blue indicator, and sugars as follows: (1) glucose, (2) fructose, (3) mannose, (4) galactose, (5) maltose, (6) sucrose, (7) lactose, (8) trehalose, (9) no addition.

The gelatine was dispensed in "18 × 150 mm." test-tubes; the carbohydrate media in large Smith fermentation tubes, and all were autoclaved at 12 pounds pressure for 15 minutes. After cooling, tubes of gelatine were inoculated in duplicate, using the stab method, and incubated at 25° C. The fermentation tubes were inoculated in duplicate with a small amount of culture taken with a hook from an agar slant and were incubated at 37° C. for five days.

In addition to the above fermentation tests, Durham fermentation tubes were prepared, using "23 × 185 mm." test-tube with a "10 × 75 mm." test-tube for a gas vial. A fermentation medium consisting of 3 per cent peptone in distilled water with brom thymol blue indicator was divided into three parts and 5 per cent quantities of the following sugars were used in each respectively: (1) glucose, (2) sucrose, and (3) galactose. The fermentation tubes were inoculated very heavily—each one being inoculated with approximately all of a slant culture which had been grown previously, using a corresponding sugar as a carbon source. It was hoped that the great number of cells initially present would provide anaerobic conditions.

Results.—Microscopic examinations of slides prepared from bits of the cultures obtained from near the center of the slants revealed, in all cases, a complex mixture of filaments with verticels of blastospores and budding yeast cells. After several days, there were also observed numerous thick-walled, round chlamydospores appearing terminally on thick filaments and free in the medium. The results of the fermentation tests with a light and a heavy inoculation used in this study are given in tables I and II, respectively.

TABLE I

ACID AND GAS PRODUCTION BY *CANDIDA ALBICANS* A.T.C.C. 2091 IN PEPTONE CARBOHYDRATE MEDIA. LIGHT INOCULUM.

Carbohydrate	Reaction	Gas
Glucose	Acid	+*
Fructose	Acid	+
Mannose	Acid	+
Galactose	Acid	—
Maltose	Acid	+
Sucrose	Acid	—
Lactose	Strongly alkaline	—
Trehalose	Acid	—
None	Strongly alkaline	—

*+, gas produced; —, no gas produced.

TABLE II

ACID AND GAS PRODUCTION BY *CANDIDA ALBICANS* A.T.C.C. 2091 IN PEPTONE CARBOHYDRATE MEDIA. VERY HEAVY INOCULUM.

Carbohydrate	Reaction	Gas
Glucose	Acid	+*
Sucrose	Acid	—
Galactose	Acid	+

*+, gas produced; —, no gas produced.

It is noted (Table I) that glucose, fructose, mannose, and maltose are readily fermented with acid and gas. It is also observed that, although galactose, sucrose, and trehalose are utilized, producing an acid and a rich growth, gas is produced in galactose (Table II) only under conditions unsuitable for further growth and in sucrose not at all. These observations will be again referred to in the discussion of nutrition and its relation to morphology. Finally, this organism brought about a complete liquefaction of the nutrient gelatin, a characteristic included by most taxonomists.

These results are thus in agreement with the taxonomic requirements presented in the literature and reviewed by Skinner (1947). According to Skinner, the most obvious morphological characteristic of this species is the production of round (or nearly so) heavy-walled terminal cells called chlamydospores. Strands of mycelium may or may not develop from which blastospores or buds are invariably produced. It is also generally agreed among mycologists that *Candida albicans* is the only species of the yeast-like fungi which ferments (produces gas) glucose, galactose, and maltose, but not sucrose and lactose.

Since all of the above characteristics are possessed by *Candida albicans* A.T.C.C. 2091, it is concluded that it is as typical a culture as can be obtained and is a suitable one for this type of study.

Influence of Hydrogen Ion Concentration

In this experiment, the basal medium was adjusted in series at pH 3 through 9 by means of a Beckman pH meter with approximately 5 per cent HCl and 5 per cent NaOH. The media were then dispensed in test-tubes suitable for slants and were autoclaved at 12–15 pounds pressure for 12 minutes.[1] In addition to this medium, Bacto yeast extract agar, corn steepwater agar, and Bacto malt-extract agar were prepared as above at pH values of 5 and 8. All media except that adjusted to pH 3 were inoculated as slants. The medium of pH 3 would not solidify after autoclaving and was inoculated by the stab method. These cultures were incubated at 24° C. for two days.

Results.—In general, there was little difference in growth of the organism in the ranges of pH 4 through 7. Growth was poor at pH 3 and 8, and no growth was noticeable on the pH 9 culture for several days. When growth did occur on this medium, it began as a little colony at the very thin part of the slant and gradually spread down over the thicker portion. When this colony was used to inoculate tubes of the same medium, growth occurred promptly.

On the basal medium at extreme pH ranges (3, 8, and 9), microscopic examination revealed a preponderance of yeast-like cells and large, spherical, thick-walled chlamydospores. The filaments that were present were of irregular shape and had a swollen appearance (pl. 15, fig. 1). The most filamentous growth occurred on the basal medium at pH 5. At ranges of pH 4 and 6, the filaments were not so regularly thread-like as those grown at pH 5, but they, like it, did not develop chlamydospores within 2 days. Although the culture grown at pH 7 was quite filamentous, it consisted of more yeast-like cells and irregular filaments than did those grown at a slightly lower pH. Chlamydospores were also numerous. Cultures on malt extract at corresponding pH ranges had very much the same morphology as those grown on basal medium. Yeast extract and corn steepwater produced a preponderance of yeast cells under all conditions.

[1] The effect of autoclaving was determined on these media and some change was observed. These changes were never over .5 of a pH unit, however, and always occurred in the direction of neutrality.

Influence of Nutrients

In order to determine the basic nutritional requirements of this organism, a series of media was prepared with each medium lacking a different ingredient of the complete basal medium. These media were prepared as slants, and each was inoculated from a stock culture maintained on glucose peptone agar. Slants of the complete basal medium were inoculated for controls. All were incubated at 24° C.

After one day's growth the slants were examined macroscopically; then bits of material taken from them with a nichrome wire hook were mounted on slides, stained, and examined microscopically. Examinations were made after two days, three days, and longer periods to determine the effect of prolonged incubation.

Results.—Macroscopic examination of the day-old cultures revealed considerable difference, not only in the amounts of growth on the various media but also in their gross morphologies. Poor, though distinct, growth was observed on media which were lacking in all vitamins, biotin alone, phosphorus, potassium, and sugar. All the other media except that lacking calcium pantothenate, which was so little different as to be doubtful, gave almost identically luxuriant growth.

The gross morphologies of the cultures resulting on these media were quite as distinctly different as the growth quantities. There was little difference in the growth resulting from lack of sugar, biotin or all vitamins, and phosphate, each being almost pure white, very soft, and creamy. The growth resulting on a potassium-deficient medium, though not so distinctly differing from the above in young culture, became rather dry and granular with a yellow-green color.[2] Samples of each of the above cultures could be very easily removed with a wire loop. The growth resulting on the rest of the media was a pale olive-buff or nearly white with a velvety appearance. These cultures were found to consist of a distinct, tough membranous mat covering the surface of the agar. It was necessary to use a wire hook to tear pieces of this membrane from the slant. With little difficulty the entire membrane could be removed intact.

When samples from the above cultures were examined microscopically, it was observed that the organism had responded to each nutritional deficiency with a distinctly different morphology. As one would expect from the lack of response to any of the vitamins except biotin, omitting biotin alone had the same effect as omitting all the vitamins. The growth on each medium consisted essentially of oval yeast cells with occasional, rather short, thick mycelial strands (pl. 15, fig. 2). The effect of the lack of sugar could not be differentiated from that obtained on a biotin-deficient medium. In this medium the only carbon source was ammonium citrate which, for this organism, is a very poor one.

Material from the phosphate-deficient medium consisted of very long mycelial strands with comparatively few typical yeast cells and blastospores. The most conspicuous characteristics were the numerous chlamydospores which developed in a very short time and the large vacuoles in the hyphae and yeast cells (pl. 15, fig. 3).

[2] Jones and Peck (1940) have reported a green pigment produced by *Candida albicans* and *C. stellatoidea.*

The potassium-deficient medium also yielded a growth form of a rather distinct morphology. Although there were practically no free yeast cells, neither was there ever a true mycelium. The entire growth consisted of clusters or rosettes of pseudohyphae composed of elongated, distinctly separate cells (pl. 15, fig. 4).

The samples from all the rest of the media were found to be just as much alike microscopically as they were macroscopically. All consisted of very dense entanglements of very long, thread-like, apparently non-septate hyphae. The cultures contained very few yeast cells and blastospores when young, but as they grew older these forms began to predominate (pl. 15, fig. 5). The effect of age will be discussed in more detail in a later section.

As indicated above, the basal medium contains several constituents which are not necessary for good growth. To test these effects further, the following medium was prepared in slants and inoculated:

Sucrose	10.0 gm.	Calcium pantothenate	1.0 mg.
$MgSO_4 \cdot 7\ H_2O$	10.0 mg.	Copper sulfate	25.0 microgm.
$MgSO_4 \cdot 7\ H_2O$	10.0 mg.	Agar	20.0 gm.
Amm. citrate (dibasic)	6.0 gm.	Distilled water to	1000.0 ml.
Biotin	2.5 microgm.		

Growth on the above medium after two days was not as heavy as that obtained on the complete basal medium, though the morphology was the same. Since it was desired to obtain the best growth possible, a basal medium was prepared, consisting of all of the heretofore-mentioned substances, except the vitamins, riboflavin, calcium pantothenate, inositol, thiamine, and pyridoxine, and asparagine.

From the data obtained on the containers of the chemicals used, it was calculated that at least the following quantities of inorganic constituents were present per liter of medium under all conditions:

Magnesium, less than .05 mg.
Phosphorus as phosphate, less than .02 mg.
Zinc, .0075 microgm.
Iron, .065 mg.
Copper, .0075 microgm.
Other sources of trace substances are from the distilled water and the agar.

Undoubtedly, most of these elements, especially magnesium, iron, and phosphorus, are required by this organism, but with the exception of phosphate, these requirements are so low that a demonstration of them is rather difficult. For information concerning the purification of media and the effects of various metallic ions on the growth and metabolism of fungi, the reader is referred to Perlman (1949).

Effects of various carbon sources.—The medium used was the basal medium previously described but with the omission of all of the vitamins except biotin, and the substitution of other possible carbon sources for sucrose. Large Durham fermentation tubes (25 ml. of medium) of the media were prepared, using 5 per cent sugars, and inoculated heavily from a culture previously grown on the complete basal medium. Since the only difference in any of the media was the carbohydrate, the complete medium is designated only by the name of the sugar.

The fermentation was at room temperature (25–30° C.). The results are given in Table III.

TABLE III

ACID AND GAS PRODUCTION BY *CANDIDA ALBICANS* A.T.C.C. 2091 IN SYNTHETIC CARBOHYDRATE MEDIA

Carbohydrate	Reaction	Gas
Glucose	Acid	++++*
Fructose	Acid	+++
Mannose	Acid	+++
Galactose	Acid	+
Maltose	Acid	++
Sucrose	Acid	—

* Relative rates of gas production are indicated by the number of plus signs; — indicates no gas production.

In addition to fermentation tests, agar slants of the same basal medium were prepared using the above sugars as well as alcohol, glycerol, starch, and succinic acid as sole sources of carbon and in combination with each other. Various quantities of each compound were used to determine the effect of concentration. These media were inoculated and incubated at 24° C. for 24 hours.

Results.—Fermentation (gas production) did not become apparent in glucose medium until after two days and not in the others until several hours later. By the end of three days, both the glucose and mannose fermentations were quite active with considerable gas production. There was a small amount of gas in the fructose fermentation tube, but in the galactose, maltose, and sucrose tubes, there was still no activity. Eventually, the maltose fermentation was active and still later the galactose, but there was no gas production from sucrose after a month.

On slants containing the above medium, with 2 per cent concentrations of glucose, fructose, and mannose respectively, there was no noticeable macroscopic difference in growth. All cultures grown on these media, after one day, were soft, creamy white, and very easily removed from the slant with a wire loop. Microscopic examinations of all three of these cultures revealed a complex mixture of yeast cells and filaments (pl. 15, fig. 6).

The cultures grown on galactose, maltose, and sucrose media were almost white, rather dry, and so tough that a wire hook was required to tear portions from the slants. The growth on the galactose culture appeared somewhat more luxuriant than that obtained on the other media, and after a few days it became quite pubescent and yellow in color. Microscopically, the growth on galactose medium was the most purely mycelial of any of the cultures obtained on these three media, although all three were composed predominantly of long, thread-like, non-septate filaments (pl. 17, fig. 18).

Lactose and starch were not utilized by this organism, and the resulting growth was like that obtained on medium containing only citrate as a carbon source. The reactions of these media became alkaline.

Alcohol, glycerol, and succinic acid were utilized but the growth was almost entirely yeast-like (pl. 15, fig. 2). Two per cent succinic acid produced the richest growth of the three. These media became alkaline in reaction.

In all cultures in which 1 per cent alcohol was added to the sugar media, the growth became more filamentous than that obtained on sugar media alone. When 3 per cent alcohol was added, however, the resulting growth was characterized by rather large yeast cells in clumps and chains, with very frequent, rather short, pseudohyphae attached, presenting many clavate structures (pl. 16, fig. 7). When 5 per cent sugar concentrations were used, there was greater tendency in all media to the yeast-like phase. Growth resulting on galactose medium was still the most mycelial of the group.

All the above cultures were examined from time to time both macroscopically and microscopically to determine the effect of age. Microscopic examination never revealed a culture which became more filamentous with age. However, to the naked eye some of the cultures, particularly those which on the first day were practically pure mycelial structures, became more hirsute after four or five days longer incubation. Those apparently thread-like strands seen by the unaided eye extending out from the edge of the colony were each composed of a single long filament very thickly covered with dense clusters of blastospores. The central filaments were too small to be seen macroscopically, but there is little doubt that they had been produced long before they could be noticed. Microscopically, any sample taken from a culture, which had been almost entirely mycelial when only one or two days old, after several days revealed a preponderance of yeast-like cells. The mycelium which was still present was apparently devoid of protoplasm since it would not stain except for occasional granular structures. It was observed that the yeast cells developed between the membranous mat produced by the mycelium and the agar, and eventually broke through to the surface as the membrane degenerated. A culture which was yeast-like at the beginning was never observed to become more filamentous with age.

Influence of Temperature

Media.—The medium used in determining the effect of temperature upon filamentation was mostly the original basal medium, but almost every other medium used in this study was tested at various temperatures at one time or another. Agar slants were inoculated in triplicate, and one of each was incubated at 24° C., 37° C., and 40° C., and examined at 24- and 48-hour periods.

Results.—On media which were previously found to produce the yeast form at 25°–30° C., there was little difference in either the macroscopic or the microscopic appearance resulting from the three incubation temperatures. In the media which had been previously found to favor a mycelial form at room temperature

there was considerable difference. Grown at 24° C., these cultures were tough and membranous; at 37° C. and 40° C., they were no longer tough and membranous but soft and creamy. Microscopic examination revealed in those cultures incubated at 24° C. very thin, thread-like filaments with few yeast cells and blastospores (pl. 16, fig. 8), and in those incubated at 37° C. and 40° C., thick, septate pseudomycelium and rather large yeast cells in rosette-like clusters (pl. 16, fig. 9). Their general appearance is much more yeast-like than those incubated at lower temperatures.

Influence of the Consistence of the Medium

Methods.—A series of liquid media was prepared as previously described but with each medium lacking one essential nutrient. Tubes of these media and of the complete medium were inoculated in triplicate, and one of each was incubated at 24° C., 37° C., and 40° C. After two days' growth, the cultures were examined macroscopically, then they were shaken to provide uniform sampling. Samples were taken with a long, dropper-type pipette and mounted on slides for microscopic examination.

Results.—Heaviest growth occurred in the complete basal medium at all temperatures. There was considerable turbidity in the upper part of the medium and a flocculent sediment at the bottom. In the biotin-deficient medium there was a flocculent mass at the bottom of the tube and no turbidity in the upper part. In cultures from which sugar was omitted and also in those from which phosphate was omitted, there was a flocculent mass which settled rapidly when the tubes were shaken. Cultures lacking potassium were very granular and settled rapidly after they were shaken. Temperature had no visible effect upon gross morphology.

Microscopically, the differences which were obtained on different liquid media at different temperatures were not so distinct as they were found to be on solid media. This was especially true of the cultures on biotin- and sugar-deficient media, which were much more mycelial than corresponding agar slant cultures. The potassium- and phosphate-deficient media produced forms like those produced on agar slants of these media. The pseudomycelium consisting of rosettes of yeast-like cells were equally noticeable in the potassium-deficient medium. The other cultures consisted of long, thread-like filaments with numerous blastospores and yeast-cells.

There was little noticeable difference in cultures incubated at 37° and 40° C. Although high temperature inhibited filamentation on the slant cultures, this factor had surprisingly little effect on liquid media. The filaments became, perhaps, a bit thicker with more of a pseudomycelial tendency.

Tubes of the above media were also inoculated and aerated for two days by bubbling air through them. These were little different from those described for the non-aerated cultures above.

In general, most of the differences noted on agar slants were present in liquid cultures but they were less distinct. The pure mycelium and yeast forms obtained on agar slants were not obtained in liquid media.

Effect of anaerobism.—Mycologists generally agree that filaments are produced as a result of reduced oxygen tension, this conclusion having been reached mainly through comparison of growth in liquid and solid media. Since filaments were found more common in liquid media than on solid, they consider the difference to be due to the difference in oxygen available to the organism under the two conditions. Wickerham and Rettger (1939), however, described the growth of *Candida albicans* on corn meal agar under what they considered reduced oxygen tension, being accomplished by placing a cover glass over a developing colony on a petri dish or on a slide covered with a thin layer of agar. Langeron and Talice (1932) found that carbon dioxide had a stimulating effect on mycelium production. In order to test further the effect of anaerobic conditions, the following experiment was performed.

The chemical reservoir of a large desiccator (21-liter capacity) was filled with 10 per cent sodium hydroxide solution. Two petri plates and two agar slants containing sucrose basal medium were inoculated by heavy streaking from a similar culture. Approximately 150 gms. of pyrogallic acid were mixed with the sodium hydroxide solution. The cultures and a lighted candle were then introduced into the desiccator and the lid replaced. To insure sealing, the lid and rim of the desiccator were well greased with stopcock grease. For controls, like cultures were prepared and incubated outside the desiccator. All were incubated at room temperature for two days before examination.

Results.—The rich growth of the cultures incubated outside the desiccator and the almost complete lack of growth of those incubated inside the desiccator indicated that anaerobic conditions had been achieved. When material from all cultures was examined microscopically, there was little detectable difference. In both cases there were long filaments mixed with blastospores and yeast cells. The anaerobic cultures contained rather large vacuoles. When the cultures that had been incubated anaerobically were placed under aerobic conditions, they soon developed abundantly. Although all the plates had been uniformly streaked over a rather large area, most of the growth was at the edges, so that a thick widening ring was formed around the outside (pl. 16, fig. 10). A halo of hyphae surrounded the outer edge of the ring, but there were few within the surrounded area. This phenomenon is undoubtedly the same as that described and photographed by Magni (1948) in his work on reciprocal inhibition of pseudomycelium formation in parallel colonies. He believed that the lack of pseudomycelial development between parallel colonies was due to the lack of nutrients.

Effects of Various Other Substances

Various factors, in addition to those just discussed, have been reported to influence the morphology of this organism. Negroni (1935) reported the influence

of phenol in producing a rough (R) type colony of *Candida albicans* approximating the R type colony of bacteria. Mickle and Jones (1939) studied the effect of lithium chloride and immune serum on dissociation. Nickerson and Jillson (1948) found that the mycelial phase of *Candida albicans* was completely inhibited by culture filtrates of *Trichophyton rubrum*. Varying concentrations of beta indole acetic acid were found by Morquer and Nystérakis (1948) to be very influential in bringing about a filamentous form. Langeron and Guerra (1939) reported the influence of so-called "elongation factors" chief of which are high concentration of carbon dioxide and substances of high molecular weight such as peptone, and nitrates. Nickerson (1950) noted an inhibiting effect of cobaltous nitrate and proflavine on cell division in *C. albicans* with the consequent production of the mycelial form. According to him, .001 M cysteine not only inhibits chlamydospore and mycelium formation (which he considers are brought about by the same factors) in his basal medium, but also counteracts the effect of cobaltous nitrate and proflavine. Most authors believe that a high carbon-low nitrogen ratio is also conducive to mycelium production.

Certain of the experiments were repeated in this study with varying degrees of success as will be indicated.

Methods.—The medium used was usually that described above, but peptone and yeast extract agar were sometimes used. Sucrose, glucose, and galactose were used as carbon sources. All of this particular phase of work was done on agar slants.

Effect of phenol.—Galactose basal media containing approximately .05 per cent and .1 per cent phenol were inoculated with *C. albicans* and incubated at 24° C. for 24 hours. Samples were taken from the slant and prepared as previously described for microscopic examination.

Results.—Macroscopically, both the above cultures were rather rough, somewhat granular, and soon became brown in color. Microscopically, these cultures were observed to consist of very thick, irregular pseudohyphae and large yeast cells. No chlamydospores were observed (pl. 16, fig. 11).

Effects of cobaltous nitrate and cysteine.—The following media were inoculated with *C. albicans* and incubated at 24° C.:

1. Basal medium less all vitamins except biotin; 2 per cent galactose; .05 per cent cobaltous nitrate.
2. Medium as above except $MgSO_4$ was increased five fold.
3. Medium like No. 1; 2 per cent sucrose; .001 M cysteine.
4. Medium as above; 2 per cent sucrose; .001 cysteine; .05 per cent cobaltous nitrate.
5. Medium as above; 2 per cent sucrose; .002 M cysteine.
6. Medium as above; 2 per cent succinic acid; .05 per cent cobaltous nitrate.
7. Yeast extract, 1 per cent; sucrose, 2 per cent; KH_2PO_4, .02 per cent; $Co(NO_3)_2$, .05 per cent.
8. Yeast extract, 1 per cent; sucrose, 2 per cent; KH_2PO_4, .02 per cent; $Co(NO_3)_2$, .1 per cent.
9. Peptone, 3 per cent; galactose, 2 per cent; KH_2PO_4, .02 per cent; $Co(NO_3)_2$, .05 per cent.
10. Peptone, 3 per cent; glucose, 2 per cent; KH_2PO_4, .02 per cent; $Co(NO_3)_2$, .05 per cent.

Results.—The above cultures were examined at the end of twenty-four hours and from time to time thereafter. In the 24-hour cultures, there were little

macroscopic or microscopic differences between Nos. 1, 2, 3, and 5 or the basal media, using the corresponding carbon sources with the cobaltous nitrate and cysteine omitted. The basal media containing sucrose and galactose as carbon sources produced a very mycelial form when cobaltous nitrate was present. Somewhat later those containing cobaltous nitrate became rough, rather granular and dry. Culture No. 2, with a high content of magnesium sulfate, remained more like the cultures previously described on basal medium.[3] Culture No. 6, using succinic acid as a carbon source, was composed almost entirely of yeast cells, and no difference could be detected due to the addition of cobalt. Cultures 7, 8, 9, and 10 were much alike but greatly different from cultures grown on basal medium or on yeast extract or peptone media not containing cobaltous nitrate. In these natural media, cobaltous nitrate showed a definite growth inhibition not noted on the synthetic media. Growth developed very slowly on these media, beginning in small granular, brownish colonies on the thin part of the slant and slowly spreading down until, after several days, the whole slant was covered. Microscopically, these cultures were observed as clumps and chains of yeast-like cells. These last four media where cobalt nitrate was omitted gave complicated mixtures of mycelium and yeast cells.

The addition of cysteine seemed to have a slight toxic effect in the concentrations used, but it did not entirely prevent filaments from forming. When cysteine and cobalt nitrate were used, the organism became more yeast-like than when either was used alone, but this would seem to be due simply to the increased concentration of toxic substances. Chlamydospores were soon observed in these cultures when one or the other or both of these compounds was added to the media. At the concentrations used in these experiments, cysteine and cobalt had little morphological effect except for slight toxicity as indicated by the roughness of the cultures and decreased growth in certain cases.

Effects of other chemical substances.—No detailed studies were made on the other supposedly influential factors previously listed. The increased concentration of peptone to 5 per cent increased mycelial production as reported by Langeron and Guerra. Substances of high molecular weight were not tried as causes for filament production, since they were not employed in the medium which gave an almost pure mycelium. The highest molecular-weight compound used in this medium, other than the sugar, was ammonium citrate, and it was found that ammonium chloride gave an equally good mycelium and approximately the same amount of growth. Since nitrates were not employed at all, it is concluded that a good mycelium can develop in their absence. As for the necessity of a high carbon-low nitrogen ratio for mycelium production, it was found that when the carbon source was raised to a higher concentration than 5 per cent, there was a great tendency toward the yeast form.

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[3] This supports the findings of Abelson and Aldous (1950) concerning the antagonism of cobalt and other bivalent ions toward magnesium metabolism. They found that nickel and cobalt were less toxic to a variety of microorganisms when the magnesium content of the medium was increased.

Chlorides.—Although the effect of chlorides was not studied extensively, the observations made in the course of this work seem to be worthy of a brief remark here and of further study in the future.

While studying the effect of potassium on morphology (KCl being the potassium source) it was observed that increased concentrations of this salt up to 10 per cent would produce a purer mycelium when glucose was used as the carbon source than would the medium containing the normal, comparatively low concentration. Since it had been previously observed that potassium was necessary for the formation of a mycelium, higher concentrations of this element were believed to account for the mycelial stimulation. However, when 10 per cent NaCl was employed, using the normal amount of KCl in a glucose basal medium, this mycelium-stimulating (or yeast- and blastospore-retarding) tendency was observed to be as strong as in the 10 per cent KCl medium.

Morphology on Various Natural Media

Skinner (1947) has listed a number of natural media employed by mycologists in their morphological studies, but he preferred Benham's corn-meal agar as prepared by Bernhardt (1946) and Anderson's corn meal infusion for inducing mycelium and chlamydospore production. Wickerham and Rettger (1939) found corn-meal agar very suitable for true mycelium production. Talice (1930) preferred potato infusion or potato agar for inducing filamentation. Sabouraud agar (glucose peptone agar) has found wide use in morphological studies, giving cells almost exclusively of the budding yeast type. Sugar-free beef peptone gelatine stabs have also been reported useful. Diddens and Lodder (1934) employed a number of natural media, among which the most used were malt extract, wort, wort agar, glucose peptone agar, and milk.

Media.—Various natural media, including Bacto malt extract, corn steepwater, yeast extract, Bacto peptone, Bacto beef, Bacto corn-meal agar, and potato and carrot decoctions, were used alone and in combination with the previously used sugars. In addition, some of these natural substances were added to the complete basal medium. These media, prepared as slants, were inoculated with a 24-hour-old culture grown on yeast extract-glucose agar at 24° C.

Results.—The malt-extract culture was the most filamentous of the group, having long, thread-like filaments with numerous blastospores. The growth of this culture was also quite heavy. Corn steepwater and yeast extract cultures were predominantly yeast-like. When yeast extract was added to the complete basal medium, which ordinarily produces the mycelial form, a yeast-like form was produced. Peptone cultures were always complicated mixtures of filaments and yeast cells. All the above media yielded fair growth, but the addition of mineral salts and sugars usually increased the growth. The Bacto beef and corn-meal agar cultures were fairly filamentous. However, most of the filaments were rather short, and in young cultures were swollen at the ends. These cultures showed very poor growth even with sugars and potassium phosphate added. The growth

on potato and carrot agar was quite good, being of the soft, creamy type. Both these cultures contained many pseudohyphae and a preponderance of yeast cells. The addition of sucrose to these media improved the growth, but the morphology was virtually unaffected. There was little better growth, if any, in any of these media than that obtained on the basal medium. In most cases it was inferior.

Morphological Comparisons of the A.T.C.C. Strain 2091 With Other Cultures of *C. albicans*

Five cultures of *Candida albicans* were obtained from Dr. Mackinnon which were without data except for the initials and numbers used to designate the individual strains. These cultures were designated as 1. H.M. 493, 1. H.M. 805, 1. H.M. 806, 1. H.M. 679, and 1. H.M. 582. Agar slants of galactose basal medium from which all vitamins except biotin were omitted were inoculated with these strains and were incubated at 24° C. for 24–48 hours. The cultures were then examined macroscopically and microscopically.

The slant culture 1. H.M. 493 was almost pure white, rather soft, and wrinkled. Microscopically, it was quite mycelial, but the hyphae were rather thick and twisted, indicating that, although the growth was quite heavy, the medium was not altogether suitable for the best growth of this organism (pl. 17, fig. 13). Culture 679 was rough, cream-colored, and quite soft. Microscopic examination revealed a fairly good mycelial growth and many somewhat lance-shaped yeast cells. Growth was good (pl. 17, fig. 14). Culture 805 did not grow very well on this medium. The growth appeared rather dry, almost white, and was easily removed from the slant with a wire loop. Microscopically, it was observed to be a mixture of yeast cells and pseudohyphae (pl. 17, fig. 15). Slant culture 806 was a very heavy, almost white, velvety growth and so tough and membranous that a wire hook had to be used to remove material from the slant. As one would expect from such a membranous material, this culture was observed microscopically to be very mycelial. The individual cells present were very narrow and rather long (pl. 17, fig. 16). Culture 582 was of a very soft, creamy, glistening white material. Growth was very rich. Microscopically, this culture was seen to consist preponderantly of small yeast cells, but there were occasional long, thread-like hyphae (pl. 17, fig. 17). Although chlamydospores are not shown in the photograph, they were later observed to occur frequently in chains of six or seven as well as individually at the tips of filaments.

The six strains of *C. albicans*, including the five Mackinnon strains and the A.T.C.C. strain 2091, differ quite distinctly in their morphologies when grown on the same medium at the same time under identical conditions. Not only are the tendencies to become yeast-like or mycelial different in degree, but the individual yeast cells and blastospores are different in shape and size. The yeast cells of cultures 582 and 805 resemble most closely those of the A.T.C.C. culture, but their mycelial tendency on galactose basal medium is less pronounced. The mycelial growth of

culture 806 is greater than is ordinarily obtained with the A.T.C.C. culture, and the blastospores and individual cells are more slender and much longer. Cultures 493 and 679 resemble the A.T.C.C. culture grown under adverse conditions. Previous morphological and physiological relationships observed on the latter strain would indicate that these organisms also have different physiological requirements.

Discussion

It is evident from the results obtained in this study, at least so far as this particular organism is concerned, that some of the factors affecting morphology given by previous authors must be somewhat modified. For the sake of clarity and convenience, these factors will be considered individually.

Influence of pH.—From the review of the literature there seems to be little agreement among the various workers concerning this factor. To the extent that extreme pH ranges exert a toxic effect which has a morphological influence on the organism, the results of this study are in agreement with those of Roux and Linossier (1890). These workers found that the toxic effect is manifested by an individualization of filaments. In the present study, however, the toxic effect of extreme pH ranges, as well as other types of toxicity, almost invariably produced yeast-like cells. As previously discussed, Talice (1930) considered this factor rather important, but that the most filamentous morphology is obtained at pH 8. According to Langeron and Guerra (1939), pH is one of the most important factors, filaments being produced in an alkaline medium, yeast cells in acid.

Since there were no precise methods employed in this study for determining relative rates or quantities of growth, the exact pH optimum is not certain. The most regular, thread-like filaments and uniformly oval yeast cells and blastospores were produced at pH 5. Increasing or decreasing the pH resulted in swollen, irregular filaments, a preponderance of yeast-like cells, and an early (2 days) appearance of the thick-walled chlamydospores. This irregular morphology having been observed constantly in media known to be unsuitable for optimum growth, it is concluded that a slightly acid range (pH 5–6) is optimum for this organism. It is thus evident that pH is a very important factor, though the range must be varied considerably to exert a very noticeable influence. This influence is probably due to the toxicity exerted upon the organism. It is, perhaps, noteworthy also that the medium soon becomes acid when a readily assimilable carbohydrate is employed. When a carbon source not so readily assimilable is used or the source is too dilute, the medium becomes alkaline. It is considered that the real, morphology-determining factor in this case is one of nutrition, but the pH changes probably have some influence also.

Influence of Nutrients.—It is generally agreed among mycologists that this particular factor is of prime importance and that filamentation occurs as a result of starvation. The idea that "impoverished" media is necessary for the production of filaments developed as a result of growing the organism on various natural

substances of unknown chemical composition. It is apparently true that most natural media which produce the filamentous form yield a rather poor growth, whereas those which produce a yeast form usually yield a heavier growth. The results obtained on natural media in this study agree with those of previous authors. The results obtained on chemically identified media, however, do not support the general statement concerning "impoverished" media and are in direct opposition to that concerning the morphological influence of readily assimilable carbohydrates.

Of the sugars used in this study, galactose gave the heaviest mycelial growth, and maltose and sucrose were better than glucose, fructose, and mannose. With the exception of sucrose, which was never fermented (gas), there seems to be a relationship between the rate of fermentation and the amount of filamentation. Those which were most readily fermented (glucose, fructose, and mannose), though producing abundant filamentation, also produced more blastospores and yeast cells than the less readily fermented sugars. The reducing sugar content within the range of 1 to 3 per cent does not appear to have the importance in cell division that Nickerson attributed to it. Galactose, also a reducing sugar, not only produced the most abundant growth, but also the most abundant mycelium.

It has been shown that good filamentation not only can occur on fairly large concentrations of readily assimilable carbohydrates, but that they are necessary for good filamentation. In addition to the necessity of carbohydrates, potassium and biotin are also essential. An absence or deficiency of any one or all of these three substances results not only in a very poor growth, but the growth which does occur is of the soft, creamy type of yeast-like morphology. Phosphorus, though essential to the growth of the organism, does not seem to affect its filamentation to a very great extent. With more highly purified chemicals than ordinary C. P. chemicals such as those used in this work, the effect of phosphorus, as well as some of the other minor elements, would undoubtedly have been more evident. The very noticeable effect of the phosphate deficiency was the very early (24 hours) appearance of numerous chlamydospores. The fact that no other deficiency produced this effect in such a short period of time indicates that the production of chlamydospores is stimulated by the exhaustion of the available phosphorus in the medium. Another obvious feature of the organism grown on phosphate-deficient medium are the numerous, large vacuoles both in the filaments and the yeast cells.

Many mycologists have observed that natural media can be divided into two groups depending upon whether they produce a yeast-like or a filamentous growth of *Candida albicans*. It has been shown in this study that those substances which produce a filamentous, though a poor growth, can be fortified with carbohydrates and inorganic salts to produce good growth without affecting the morphology of the organism—that is, a heavy filamentous growth. On the other hand, no amount of fortification has been found suitable for inducing a yeast-producing natural medium to produce filaments. When a yeast-producing substance such as yeast

extract is added to a complete synthetic medium which produces abundant filamentous growth, the resulting growth is soft, creamy, and yeast-like, but little heavier than that obtained on synthetic medium alone. The results of these experiments indicate that most natural media contain various unknown substances which induce a yeast-like morphology in *Candida albicans*. That there is ample available carbon in these substances is shown by the rich growth which occurs upon them without additional carbon sources. It is doubtful that these substances are sugars since the metabolism of the organism brings about an alkaline reaction instead of the characteristic acid of carbohydrate metabolism. It is perhaps true that these natural media may contain so much nitrogenous material that the ammoniacal products of metabolism may mask the acidity given off by the carbohydrate metabolism. However, one pure natural substance, succinic acid, was readily utilized as a carbon source, and the medium became alkaline. The resulting morphology on this medium was yeast-like. There are doubtless other substances in natural material which serve as carbon sources for this organism and produce the yeast-like form.

It is then necessary to modify or perhaps do away with the term "impoverished" media when referring to media necessary for producing mycelium in *Candida albicans*, since a filamentous growth can also be a very rich growth.

Influence of temperature.—Except in liquid media where there was little detectable difference, a high temperature (37–40° C.) produced a very strong tendency toward the yeast phase. The only explanation for the discrepancy between this finding and that of other authors is that we are evidently using different organisms. If this be true, then a better description of the organism is needed, since the characteristics of this one have fulfilled all the morphological and biochemical requirements listed by the taxonomists.

Effect of the consistence of the media.—It has been observed, almost from the first study made on this organism, that the mycelial tendency is stronger in liquid than on solid media. We found this especially true in a medium which usually produced a yeast-like morphology in the solid state. The other factors, such as temperature and even nutrition, were not so obvious in their effects, though they were usually noticeable. This effect is generally attributed to the reduced oxygen tension in liquid media, but it is not so easily proven. In this study it was found that the organism could not grow anaerobically on agar. In liquid media the growth seems to occur mainly at the top and then precipitates to the bottom in a cottony mass. Indeed, if one is careful not to shake the culture tube, the mass of the organism is seen to be located in two separate places—one very fine mass at the top and the characteristic cottony mass at the bottom. The liquid between these two masses is often practically clear. By means of a dropper-type pipette, samples of each were obtained separately for microscopic examination. The examination of young cultures revealed short, highly branched chains of yeast cells at the top and long thread-like filaments at the bottom. From these experi-

ments, it seems that filaments produce clumps at the top of the medium which settle to the bottom, leaving space for individual yeast cells or blastospores to begin the process over again. The little clumps of pseudomycelium seem able to grow for a short time after sinking further into the medium, producing the typical filaments. Regardless of what the true process is, the growth cycle is not essentially different from that obtained on solid media. The filaments are produced in abundance only in young culture, and as the culture ages, the filaments degenerate until the culture becomes a granular mass composed almost entirely of yeast cells.

The effect of solid media is just as difficult to interpret as that of liquid media. Wickerham and Rettger (1939) believed that placing a cover-slip over a developing colony created the reduced oxygen tension necessary for filament formation. However, we observed the zone of filamentation consistently on the outer edge of a developing colony on petri-dish cultures which were not covered with cover-slips. Observations on a giant colony reveal that the spread is accomplished by this ever-widening zone of naked filaments which soon become covered with blastospores but never covered all the way to the tips (pl. 16, fig. 12). If reduced oxygen tension favors the production of filaments and retards the production of blastospores, it is rather strange that practically all the filamentous growth is toward the outside of a colony while blastospores are produced nearer the center where competition for oxygen would be much greater. This may be observed in the samples taken at various distances from the center of a giant colony, and the effect is even more striking when a two-inch square of an agar plate is evenly streaked with a culture of *Candida albicans*. The inner zone contains practically nothing except yeast cells, while the outer zone grows like a giant colony producing a luxurious, filamentous growth upon which blastospores develop (pl. 16, fig. 10).

The above descriptions are typical of growth obtained on good filament-producing media. When a poor mycelium-producing medium is used such as succinate basal medium the results become confusing. The growth on slants, as previously observed, is almost entirely yeast-like with only occasional filaments. In a giant colony, though the center is yeast-like as expected, there is also an outer zone of filaments. However, instead of being on the surface as they are in the carbohydrate basal medium, all seem to be growing down into the agar. They become covered with a sleeve of blastospores which makes them visible macroscopically. It is believed that this phenomenon and those previously described in liquid media have led to the conclusions in regard to anaerobism.

The relationship between the ability of the organism to produce filaments and its ability to produce gas (anaerobic fermentation) on a particular substrate should also be considered. In every case there was better mycelium production on those sugars (galactose, maltose, and sucrose) which were fermented very slowly than on those (glucose, fructose, and mannose) which were rapidly fermented. Also, in five tubes each of glucose and sucrose broth inoculated with one loop of suspension from the same inoculum and incubated in the same rack, the sucrose cul-

tures could quite easily be distinguished from the glucose because of their more abundant growth. This indicates not only that anaerobic fermentation fails to help in the production of a mycelium, but it also lowers the efficiency of the sugar utilization. From my observations it is therefore concluded that, with the proper medium and incubation at the proper temperature, comparable results are obtained on liquid and solid media.

Effects of adding various substances to the basal medium.—In general, substances not required by the yeast but which influence its morphology are of two types: (1) those which show their toxicity by retarding growth; and (2) those which do not appreciably influence the quantity of growth but influence the morphology of the organism.

There are, of course, numerous known chemicals of the first type—phenol, various metallic ions such as cobalt, etc., if used in too high concentrations, and anions such as iodide and chloride. Their toxic effect on morphology is nearly always toward the yeast form but there are evidently exceptions. High concentrations of chlorides were found, in this study, to inhibit growth somewhat and also seemed to inhibit the development of blastospores so that a purer mycelium was obtained. This may have been the result of the high osmotic pressure exerted by these salts. High concentrations of sugar, however, have the opposite effect on morphology. Nickerson (1950) found that he could suppress the yeast cells and obtain cultures of almost pure mycelium with dilute concentrations of cobaltous nitrate. The second type of substances are chemically unidentified compounds contained in varying amounts in most natural media. The chemical separation and identification of these substances are not within the scope of this study, but their presence is easily demonstrated by adding a bit of natural material such as yeast extract to a complete basal medium and observing the change in morphology exhibited by the organism.

Morphological comparisons of various strains.—If one is to accept all of the strains of yeast-like fungi that various taxonomists have placed in the species *Candida albicans,* he must accept also a great variety of morphologically and probably biochemically different characteristics of the organism. Considering that there are only three criteria upon which one can base his classification—namely, production of terminal chlamydospores; fermentation of glucose, fructose, mannose, and maltose, but not sucrose; and production of filaments—there is little wonder that he is unable to choose any typical organism for his study and have the results agree with those of another mycologist supposedly working with the same organism. Mackinnon (1940) would explain most of these differences as being due to spontaneous variation or dissociation, so that if pure yeast cells are chosen as one extreme and pure filaments as the other, a given strain may have undergone any amount of dissociation which would determine its yeast to filament ratio. If one accepts this as the cause for the differences in all the so-called "strains" of *Candida albicans,* he must also accept the fact that the shapes of the yeast cells and blastospores change considerably. Of the Mackinnon strains, there were at least three

different cell shapes. That these strains were not all satisfied nutritionally is indicated by the swollen, knobby appearance of the filaments. Perhaps, if all of these strains were derived in his laboratory from the same culture, the organism would be so protean that it is impossible to attribute to it any more than the three characteristics given.

With the organism employed for this particular study, the results do not indicate that it is as variable as indicated by Mackinnon. It is true that when this organism was streaked on plates, there were often the two types of colonies described by Mackinnon—the prickly, firm colony that could only be removed intact and the soft, creamy colony. When these aged, however, or were broken up and transferred to slants, there was little difference in their macroscopic or microscopic appearance. Either the filamentous form or the yeast-like form of each was obtained, depending upon the medium upon which they were cultured. The requirements for filamentation were the same for each and the blastospore shape never varied.

Finally, it is observed that an organism is better characterized after the second or third transfer on a given medium in 24- to 48-hour periods. The first transfer, in many cases, does not usually produce an organism greatly different from that upon which it was previously growing, particularly if one does not wash the inoculum thoroughly before using it. It is well known that microorganisms store up some critical materials, especially certain vitamins or growth factors, in sufficient quantity to suffice them for one or two generations on media lacking these elements. The first generation, therefore, may indicate not only the effect of that particular medium, but also that of the stock medium. There is another good reason for two or three successive transfers, if one wishes to study the organism under maximum conditions. The lag phase is virtually eliminated by such frequent transfers, and the organism is maintained at its maximum growth rate.

Summary

In order to determine what factors were influential in determining the morphology of the highly variable *Candida albicans*, a chemically defined medium was utilized. Since this medium was readily modified in various specific ways, it was possible to attribute any morphological change to a definite change in the culture conditions. By varying not only the constituents of the medium, but also the physical factors such as temperature and consistency, quite definite conclusions could be reached. In general, it was found that *Candida albicans* A.T.C.C. 2091 requires for filament production a readily assimilable, but not so readily fermented carbohydrate. It also requires phosphorus, potassium, and biotin. The optimum temperature for filamentation is 25–30° C. The optimum pH is near 5. Filaments are produced most abundantly during the maximum growth phase.

The yeast-like phase results from lack or deficiency in any of the above nutrients, a high temperature (37–40° C.), especially on solid media, unfavorable pH range, and toxic substances. Many natural substances contain unidentified

products which, though not growth-inhibiting, produce the soft, creamy, yeast-like form. Yeast-like forms predominate in the lag and decline phases of a culture as the filaments undergo degeneration.

Chlamydospores are produced as a result of unfavorable conditions such as too high or too low pH, deficiency of phosphorus, and to a less extent other deficiencies which are necessary for maintenance of normal growth.

The effects of liquid media on growth, especially as it pertains to reduced oxygen tension, were indefinite. The organism grew poorly, or not at all, in an anaerobic jar on solid media. On liquid media, the growth was observed on top of the medium from whence it precipitated, leaving room for more such growth. Growth on sucrose medium which, if fermented at all, is admitted to be very slow, was considerably better than that obtained on the readily fermented glucose. The sucrose medium in every case produced the greater proportion of filaments.

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Explanation of Plate 15

Candida albicans

Fig. 1. Effect of a high pH (9). Note the numerous yeast-like cells, the chlamydospores, and the few scattered filaments, × 213. Incubated at 24° C.

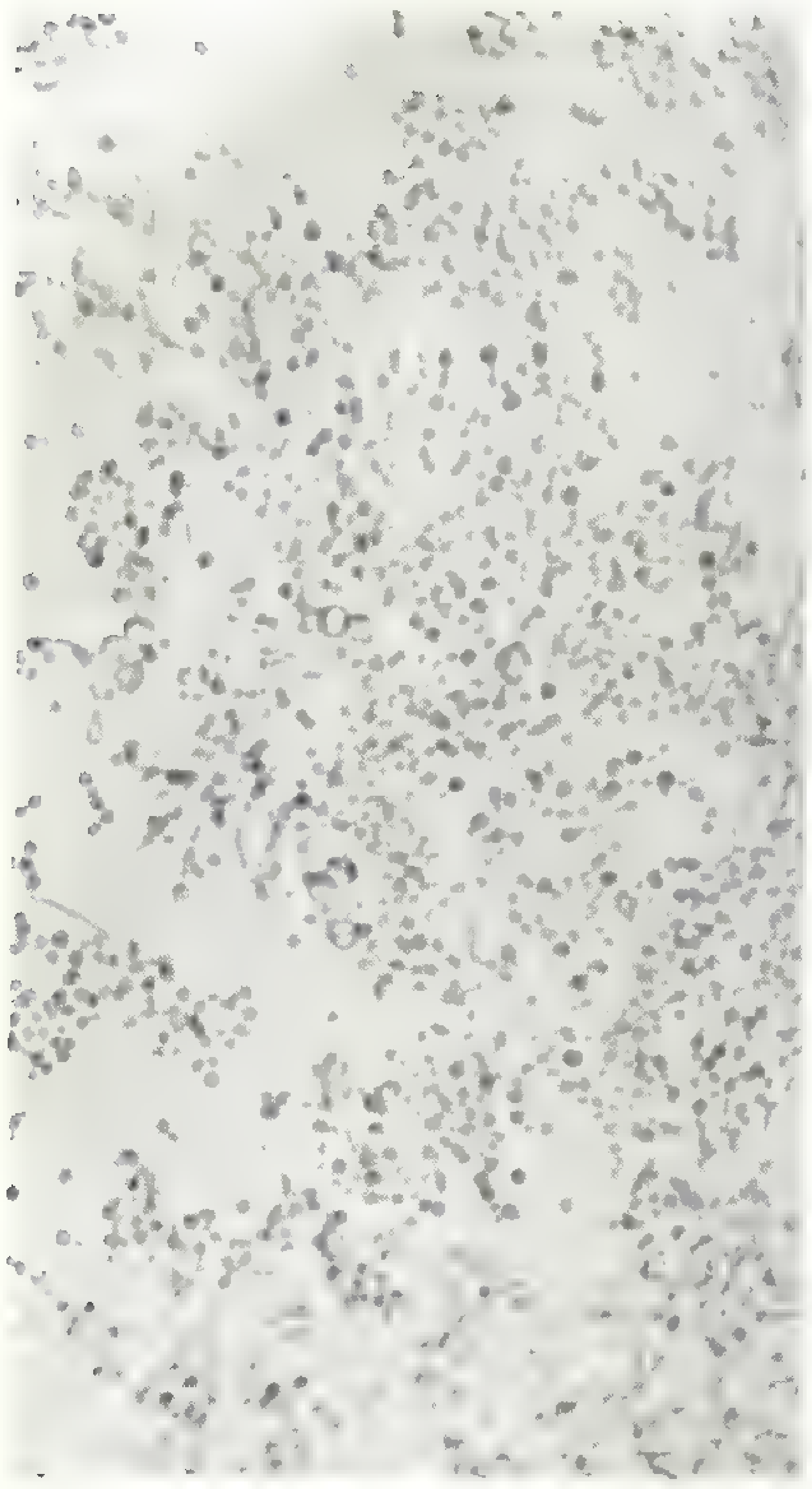
Fig. 2. Growth on approximately 2 per cent succinate basal medium for 24 hours at 24° C., × 213. The same morphology is obtained on histin and carbohydrate-deficient media.

Fig. 3. Growth on a phosphate deficient basal medium 24 hours at 24° C., × 213. Note the fairly numerous chlamydospores and yeast-like cells.

Fig. 4. Rosette-like clusters of short pseudohyphae resulting from a potassium deficiency, × 213. Grown on 2 per cent sucrose basal medium at 24° C. for 48 hours.

Fig. 5. Heavy mycelial growth resulting from growth for 24 hours incubation at 24° C., × 213. Maltose medium produces the same morphology.

Fig. 6. Growth on 2 per cent glucose basal medium for 24 hours at 24° C., × 213. Mannose and fructose media produce the same morphology.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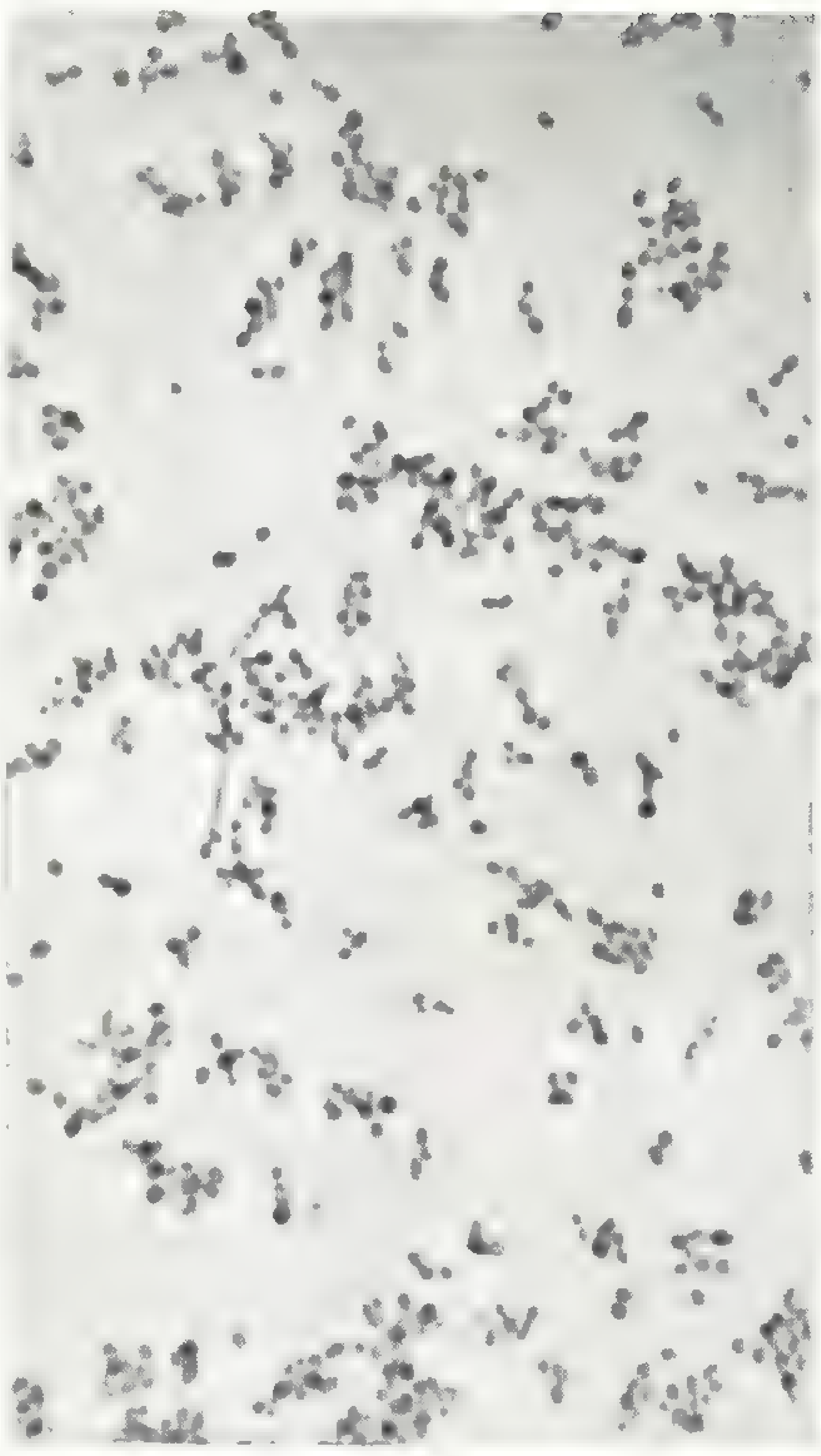
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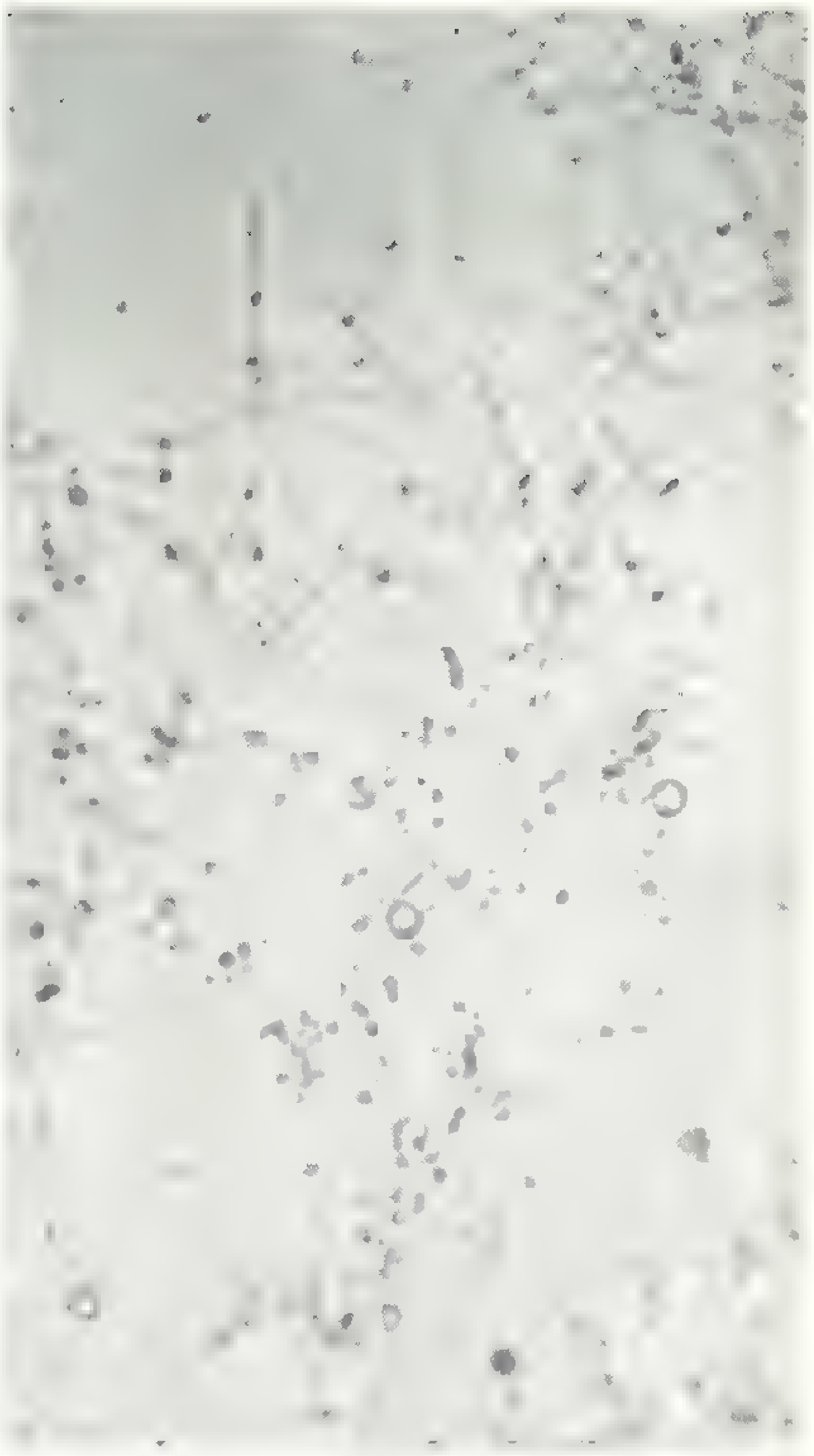
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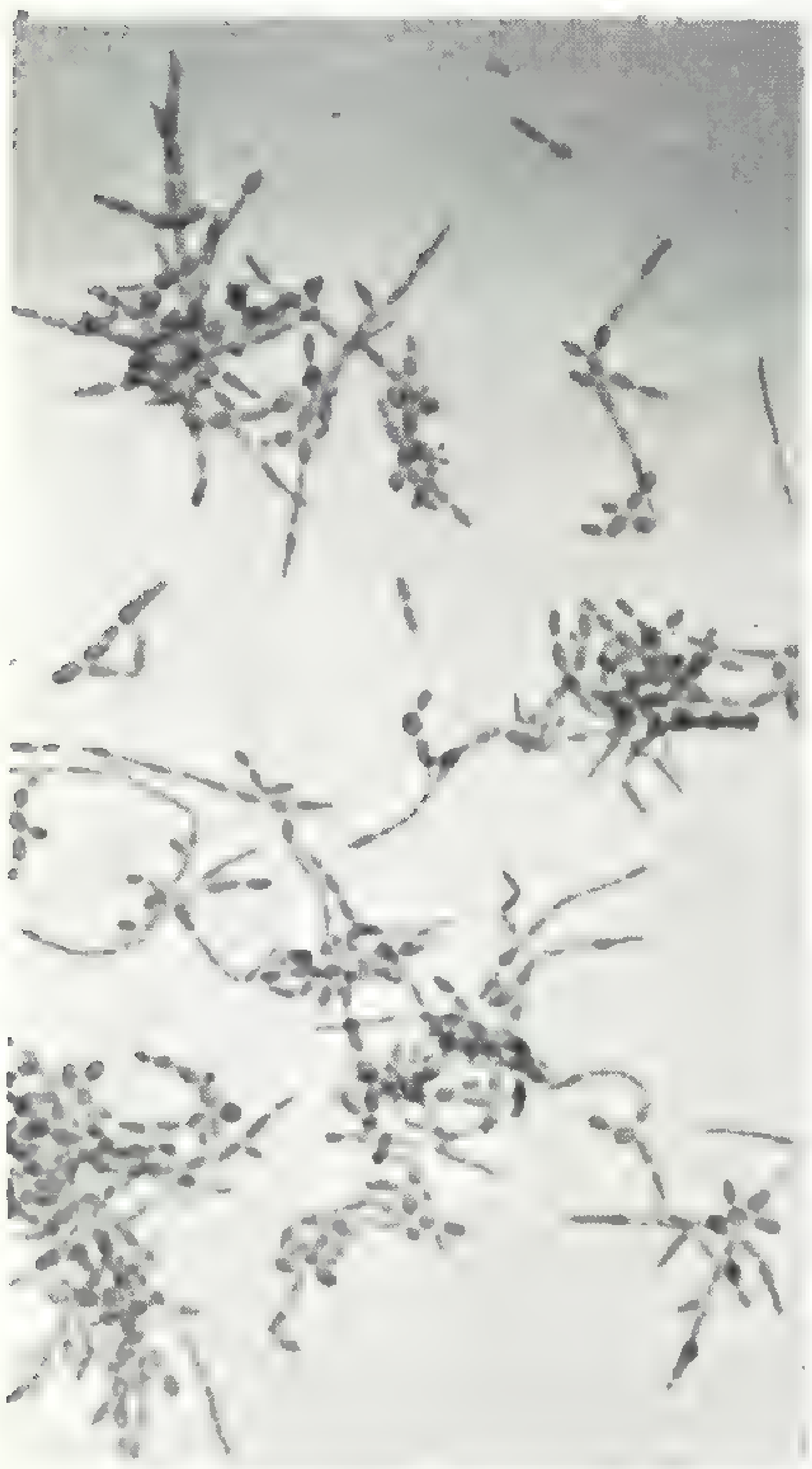
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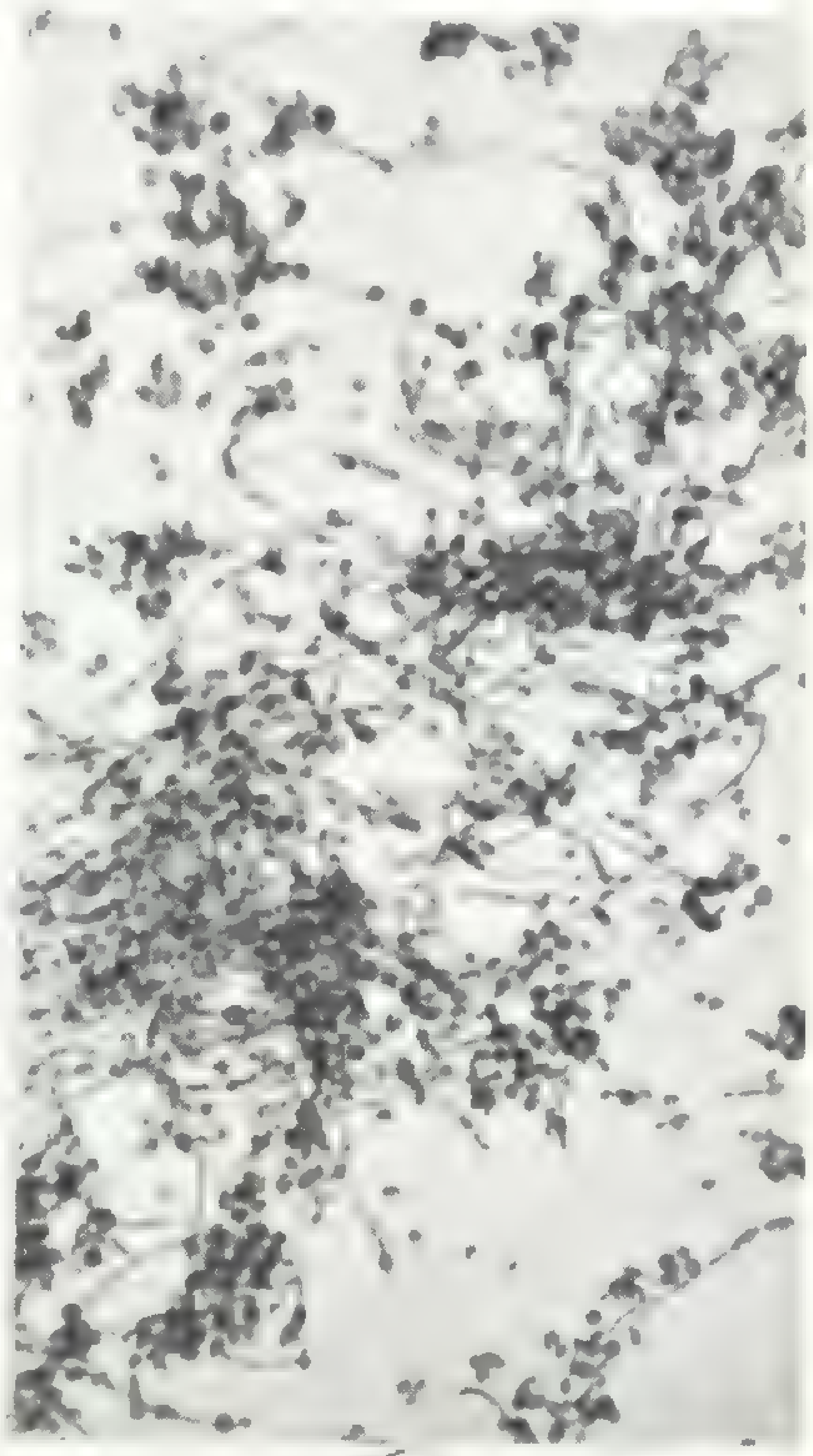
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McCLARY—*CANDIDA ALBICANS*

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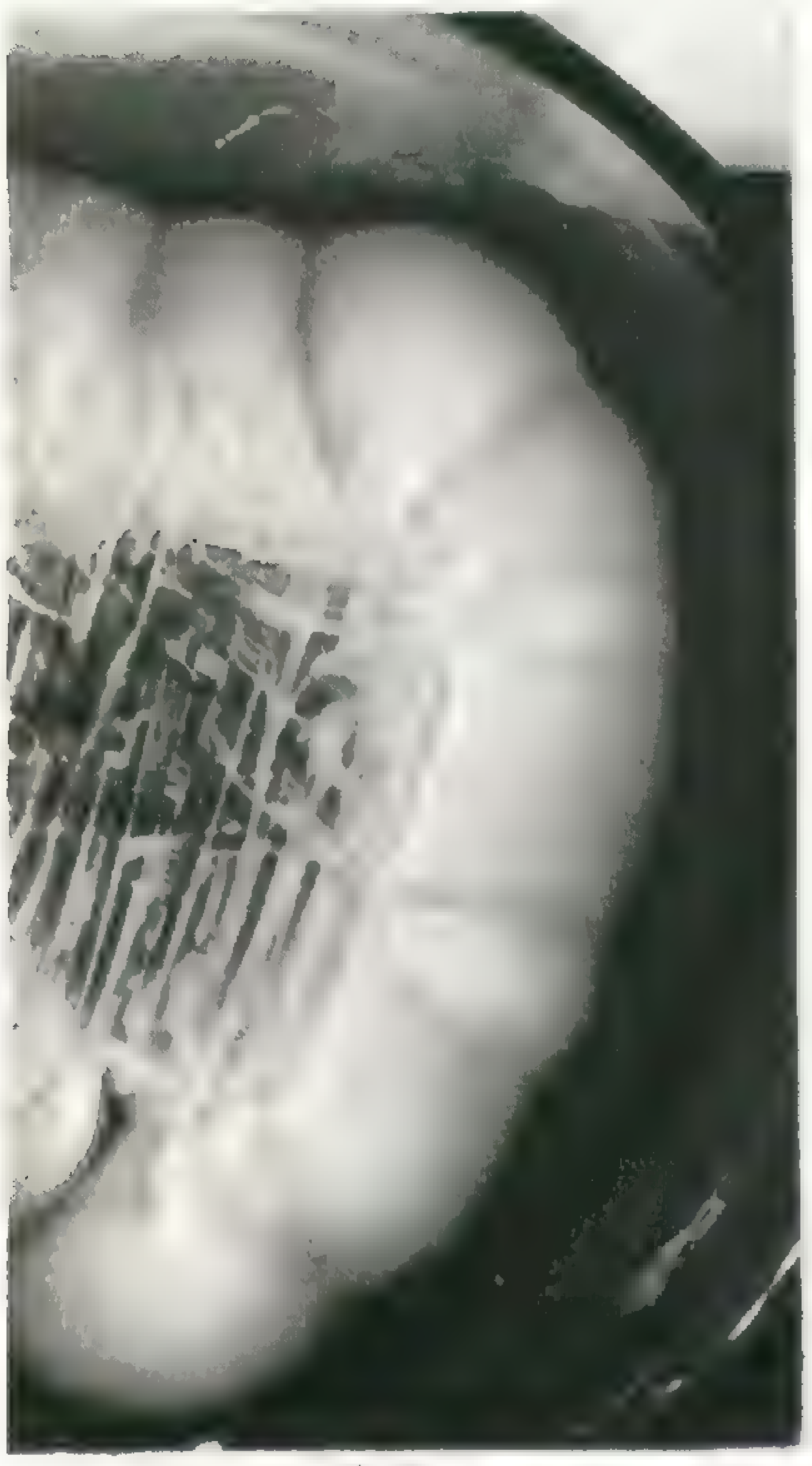
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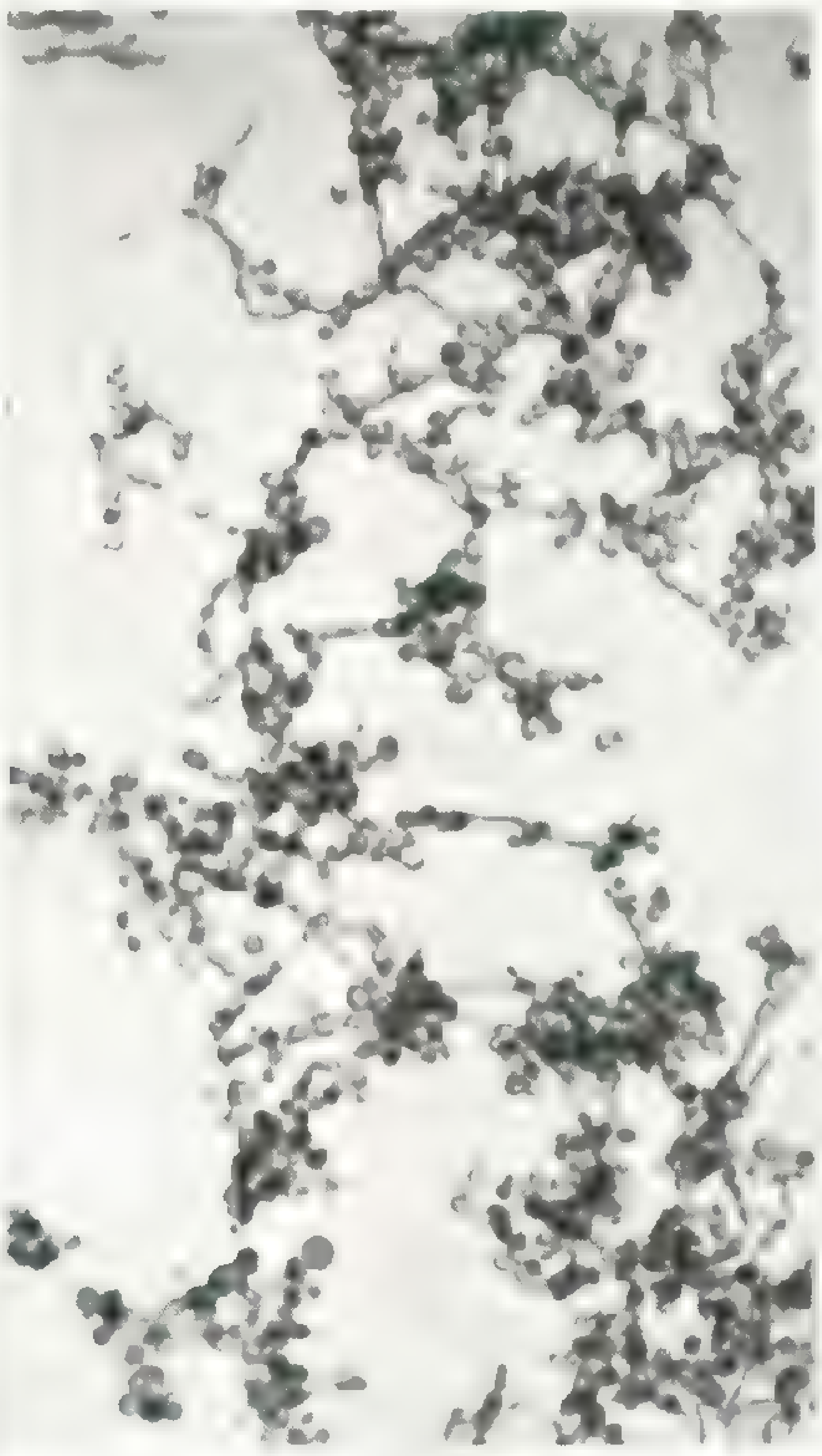
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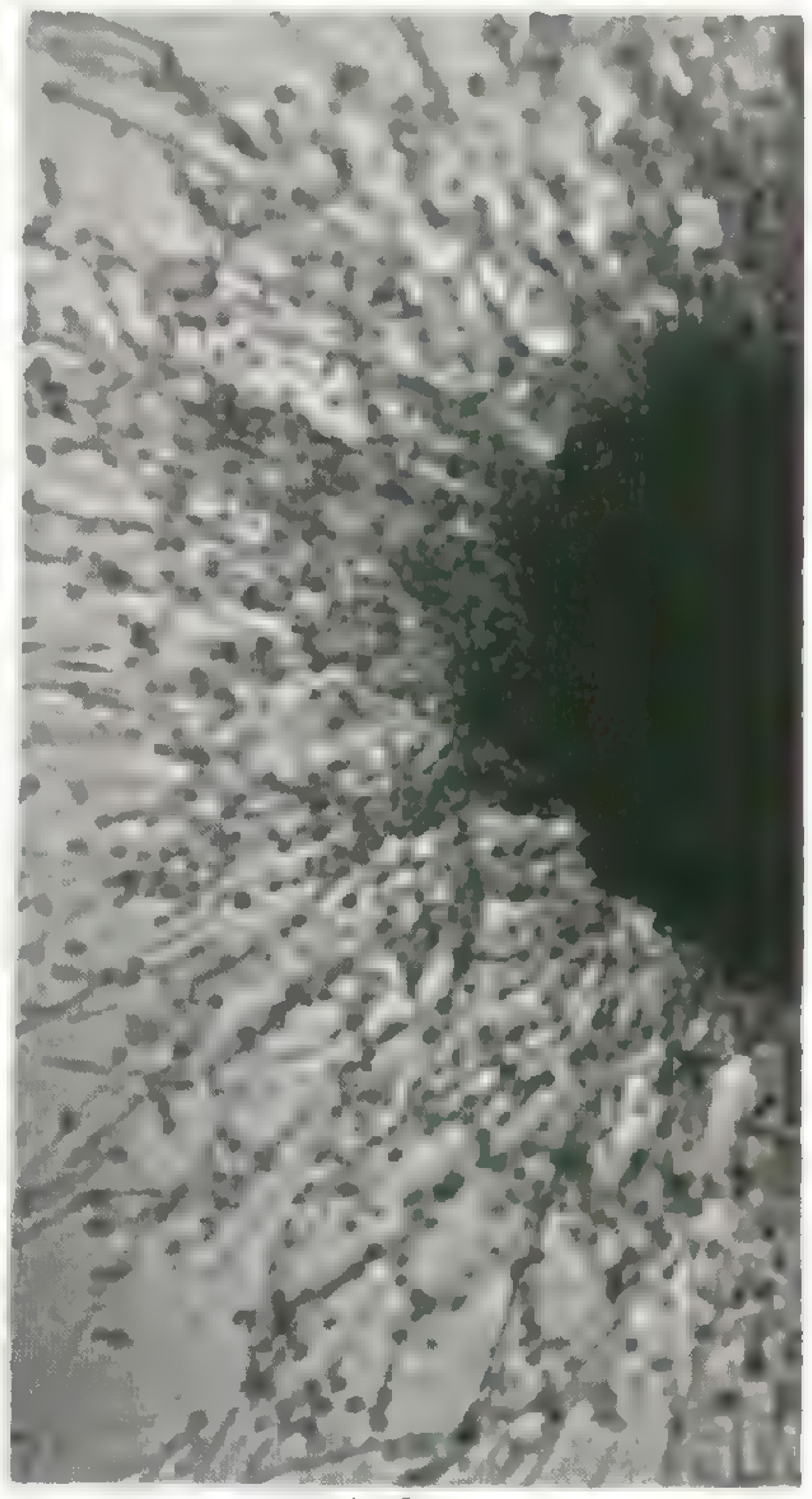
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McCLARY—*CANDIDA ALBICANS*

Explanation of Plate 16

Candida albicans

Fig. 7. Culture 24 hours old grown at 24° C. on galactose basal medium containing 3 per cent alcohol, × 213. Much the same morphology was obtained on sucrose and glucose medium containing the same quantity of alcohol, but the filaments were not so long, and typical yeast cells were more numerous.

Fig. 8. Showing effect of a high chloride content in the medium—24 hour growth on glucose basal medium containing 5 per cent potassium chloride, incubated at 24° C., × 213. Compare with fig. 6. Sodium chloride produces the same effect.

Fig. 9. Showing effect of temperature, incubated at 40° C., × 213. Medium and incubation time were the same as for fig. 8.

Fig. 10. A 20-day-old culture on an evenly streaked petri dish, × 820—grown on 2 per cent sucrose basal medium. Note the very scanty, yeast-like growth in the center and the heavy ring at the edge with filaments radiating toward the outside.

Fig. 11. Showing effect of toxic substance, × 213. Growth on basal medium containing .05 per cent phenol.

Fig. 12. Cover-slip culture of a colony several days old which developed from a single yeast cell, × 213. Grown on 1 per cent glucose basal medium at room temperature.

Explanation of Plate 17

Candida albicans

Fig. 13. Mackinnon culture 1. H. M. 493 grown on salts of basal medium, biotin, and 2 per cent galactose, × 213. Incubated for 24 hours at 24° C. Note the twisted, irregular filaments which may indicate that this medium is not entirely satisfactory for this organism.

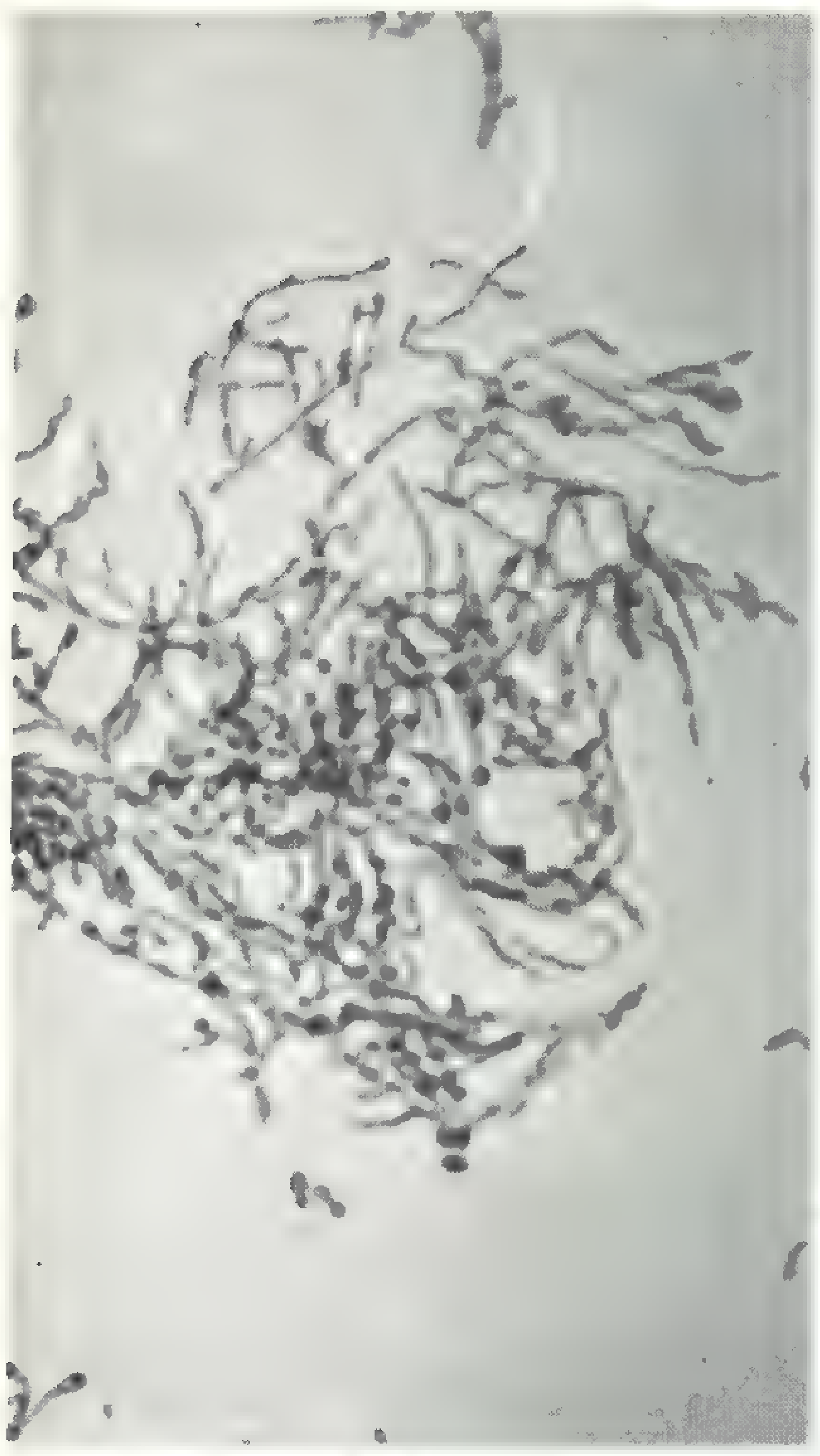
Fig. 14. Mackinnon culture 1. H. M. 679, × 213. Note the rather twisted filaments and the pointed yeast-like cells. Culture conditions identical to the above.

Fig. 15. Mackinnon culture 1. H. M. 805 grown as above, × 213. Note irregular filaments and the long, almost cylindrical individual cells.

Fig. 16. Mackinnon culture 1. H. M. 806, × 213. Note the long, regular filaments and the very long individual cells.

Fig. 17. Mackinnon culture 1. H. M. 582, × 213—almost entirely yeast-like under all conditions tried. Culture conditions here the same as above.

Fig. 18. American Type Culture Collection strain 2091 grown under the above conditions, × 213.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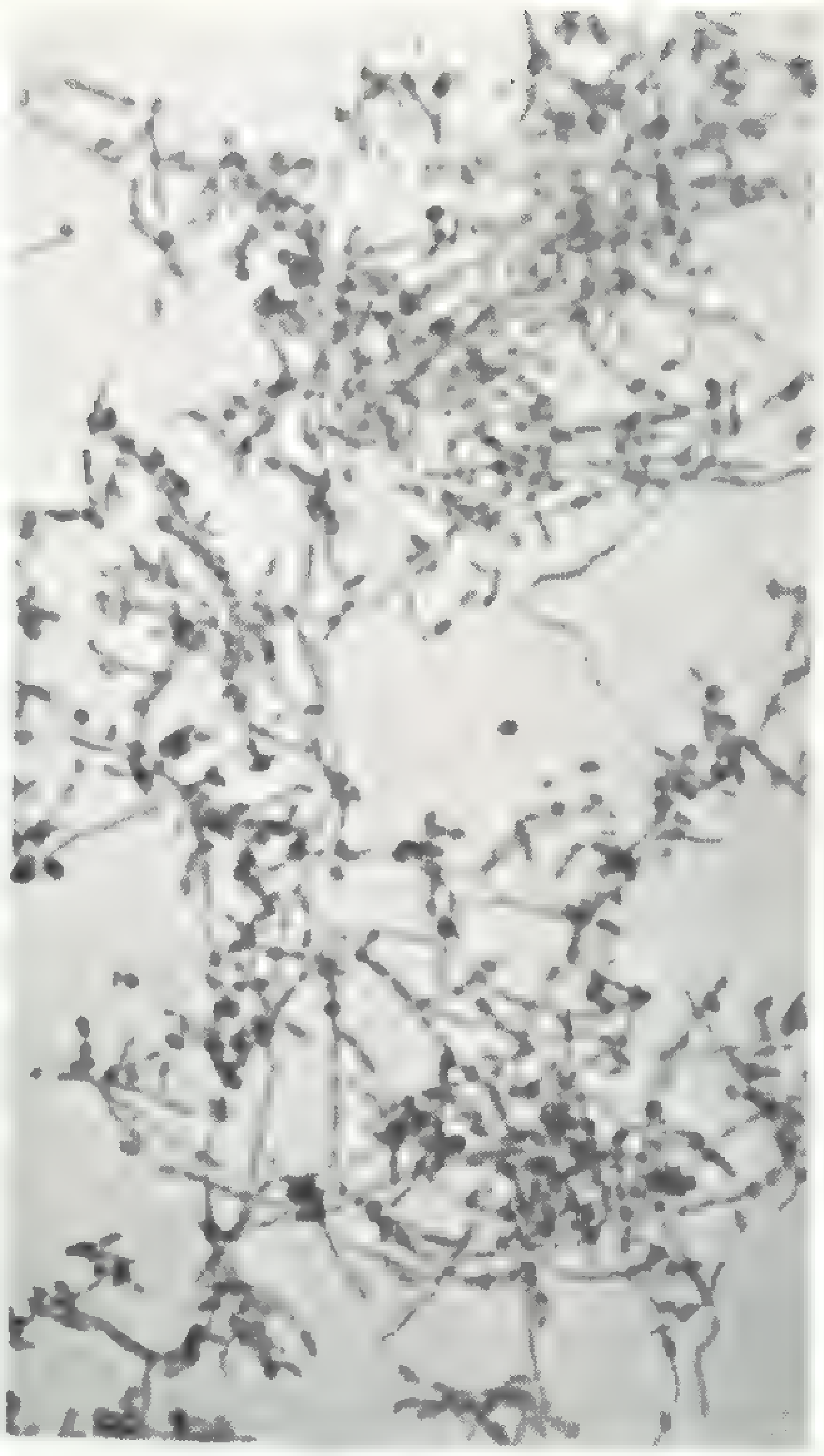
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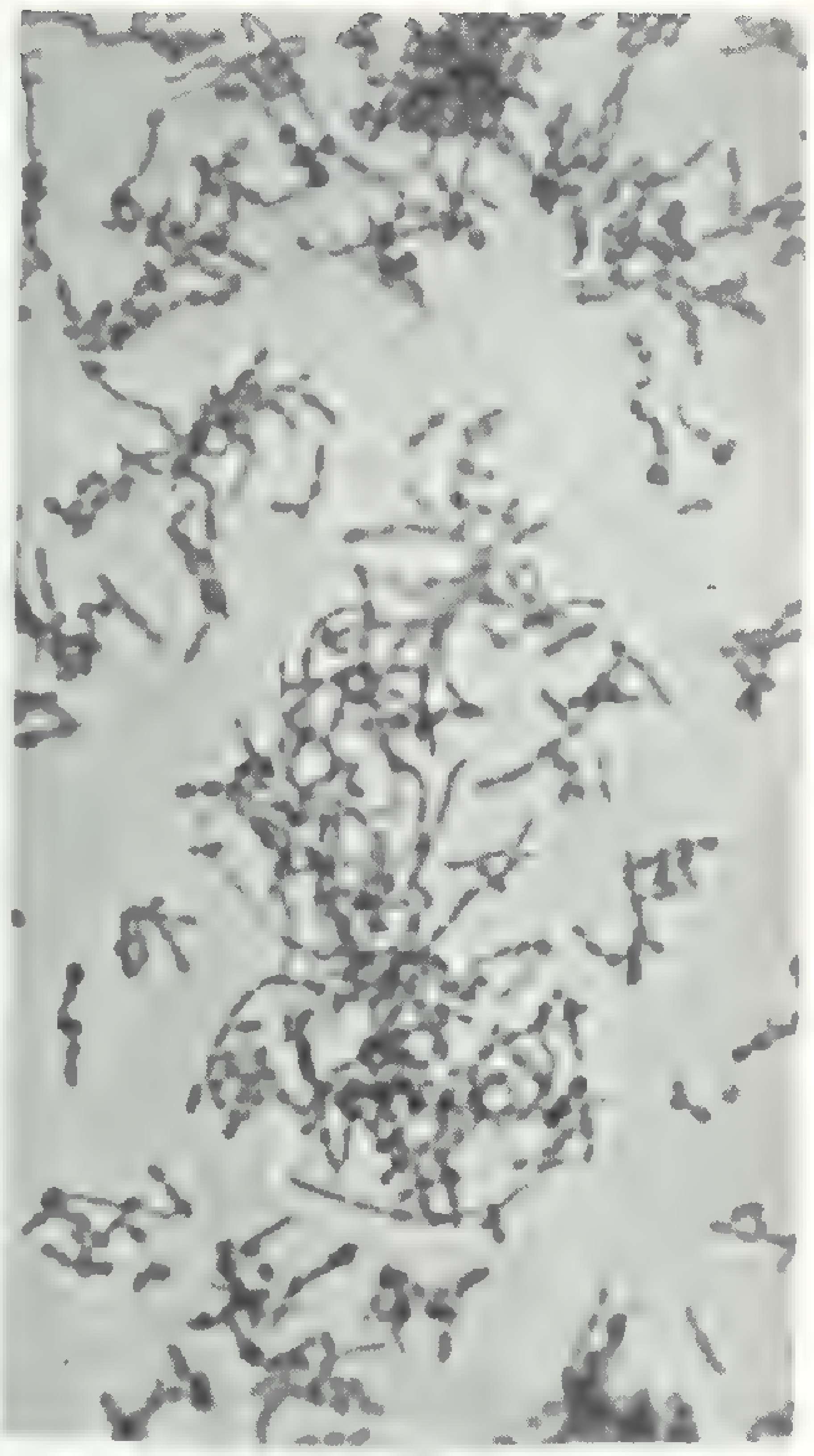
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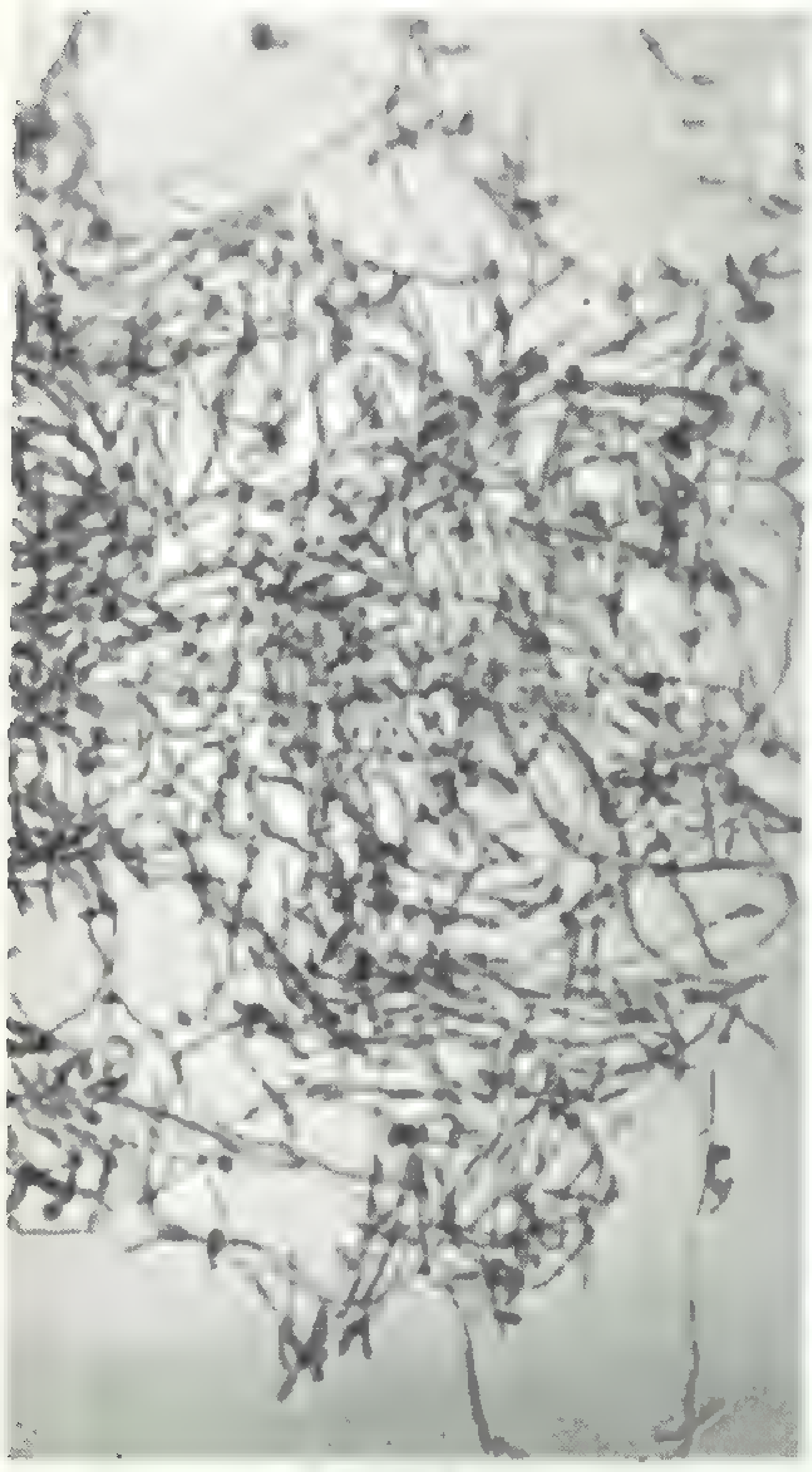
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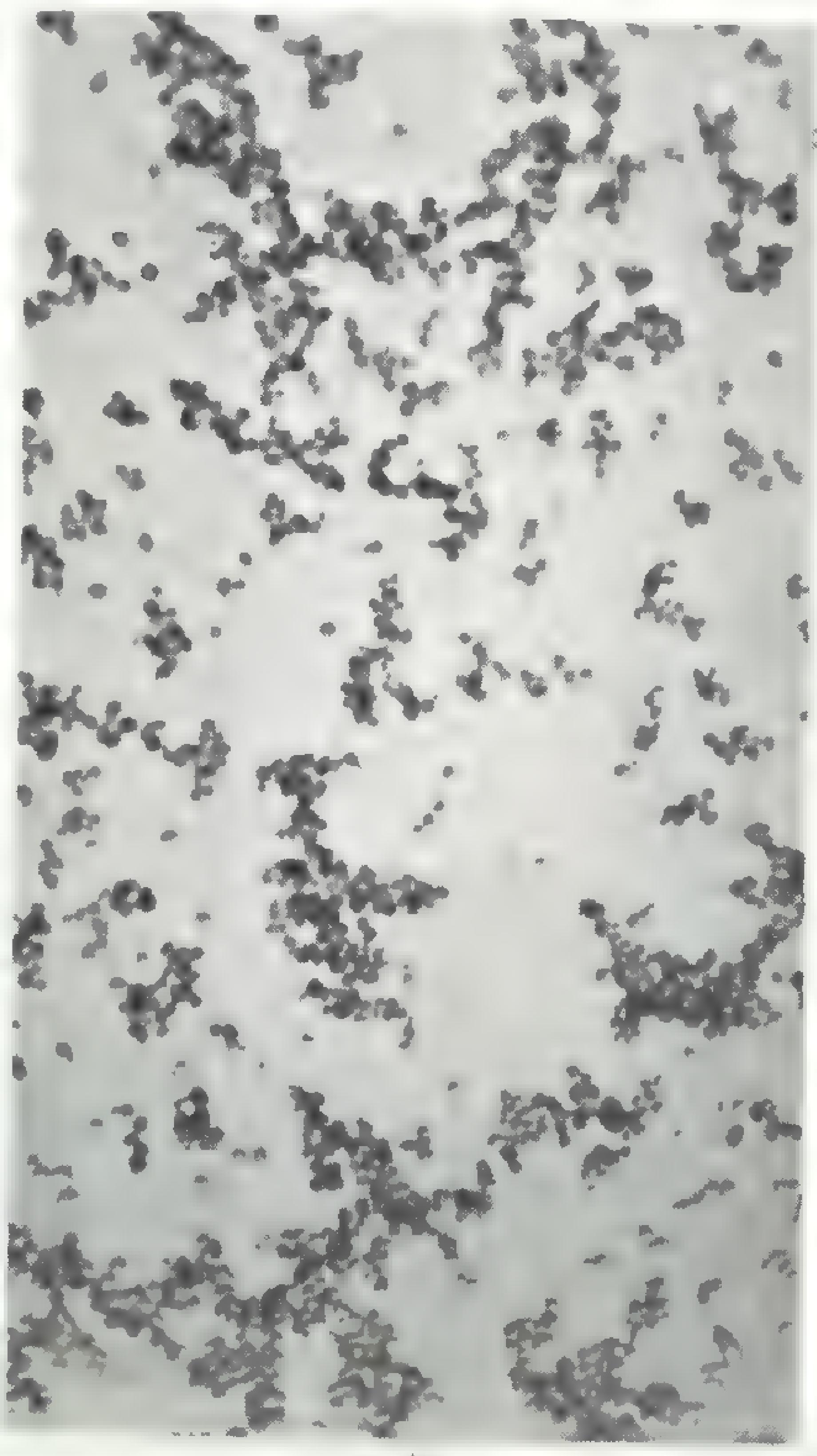
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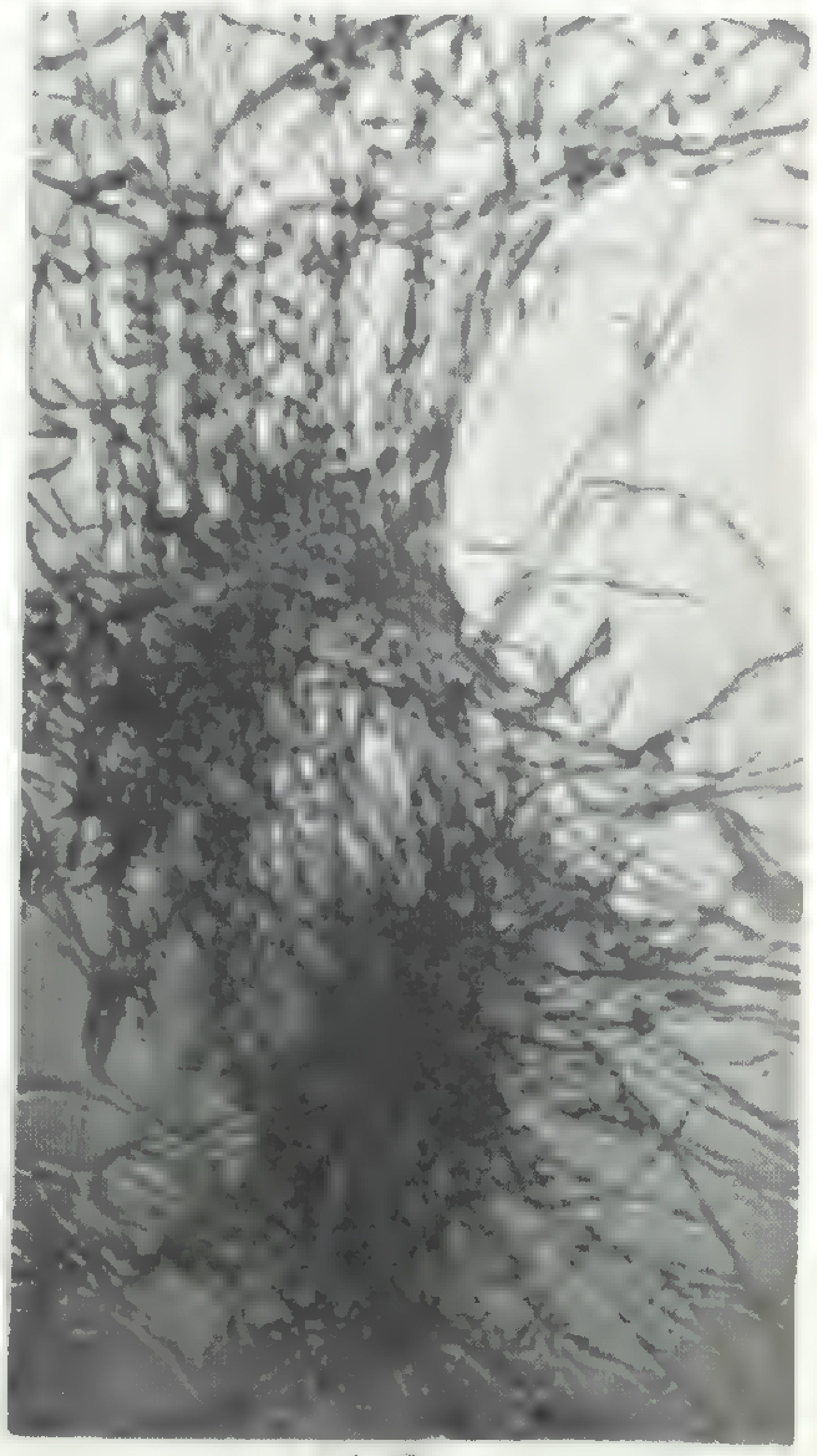
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McCLARY—*CANDIDA ALBICANS*

FOREST QUADRAT STUDIES AT THE ARBORETUM AND OBSERVATIONS ON FOREST SUCCESSION

LOUIS G. BRENNER, JR.*

Recently some of the general changes, based on time-lapse studies, occurring in the Forest Preserve of the Missouri Botanical Garden Arboretum, at Gray Summit, were reported on.[1] However, this report covered the Forest Preserve as a whole, and the complex structure of the forest growth was not expressed. Quadrat studies of critical tree associations were begun concurrently with the more general mapping of forest growth, with a view toward acquiring data on the specific changes taking place on smaller, accurately plotted sites which might be expected to lead to an understanding of the problems of forest tree associations in that area. In this paper the changes which have occurred in a lapse of twelve years are reported for three quadrats, and a fifteen-year record is available for one quadrat.

Quadrats, 15 $\times$ 15 meters, were selected in areas typical of the several recognized forest-tree associations. All corners of the quadrats were marked with painted iron stakes to insure their accurate location. A grid of stout twine was established at three-meter intervals in order to plot the trees. Approximate trunk diameters (DBH) were measured in inches so that relative dominance of forest species and their growth rate might be recorded.[2]

Quadrat in the Oak (Quercus sp.*) Coppice.*—This quadrat (figs. 1 and 2), representing a 15-year sequence, was established in an oak coppice where stump sprouts indicated that White Oak *(Quercus alba)* was the dominant tree. Soil of this area is of the Union Silt Loam and lies upon the "cotton rock" phase of the Cotter Formation of dolomitic limestones. Exposure is to the east, and the quadrat is near the summit of the ridge. The early map of the quadrat shows a more "open" aspect. At that time abundance of light encouraged the White Oaks to develop a low and spreading crown. The Red Cedar *(Juniperus virginiana)*, Redbud *(Cercis canadensis)*, Walnut *(Juglans nigra)*, Shingle Oak *(Quercus imbricaria)*, Mocker-nut Hickory *(Carya tomentosa)*, and Persimmon *(Diospyros virginiana)* assumed similar growth habits. There were a number of Slippery Elms *(Ulmus fulva)* seedlings, and a small Sycamore *(Platanus occidentalis)* in rather poor condition.

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[1] Beilmann, A. P., and Brenner, L. G. The changing forest flora of the Ozarks. Ann. Mo. Bot. Gard. 38:283–291. 1951.

[2] Species names mentioned in this report are according to Alfred Rehder's, Manual of Cultivated Trees and Shrubs, 2nd ed. 1940.

* Assistant Manager, Missouri Botanical Garden Arboretum, Gray Summit.

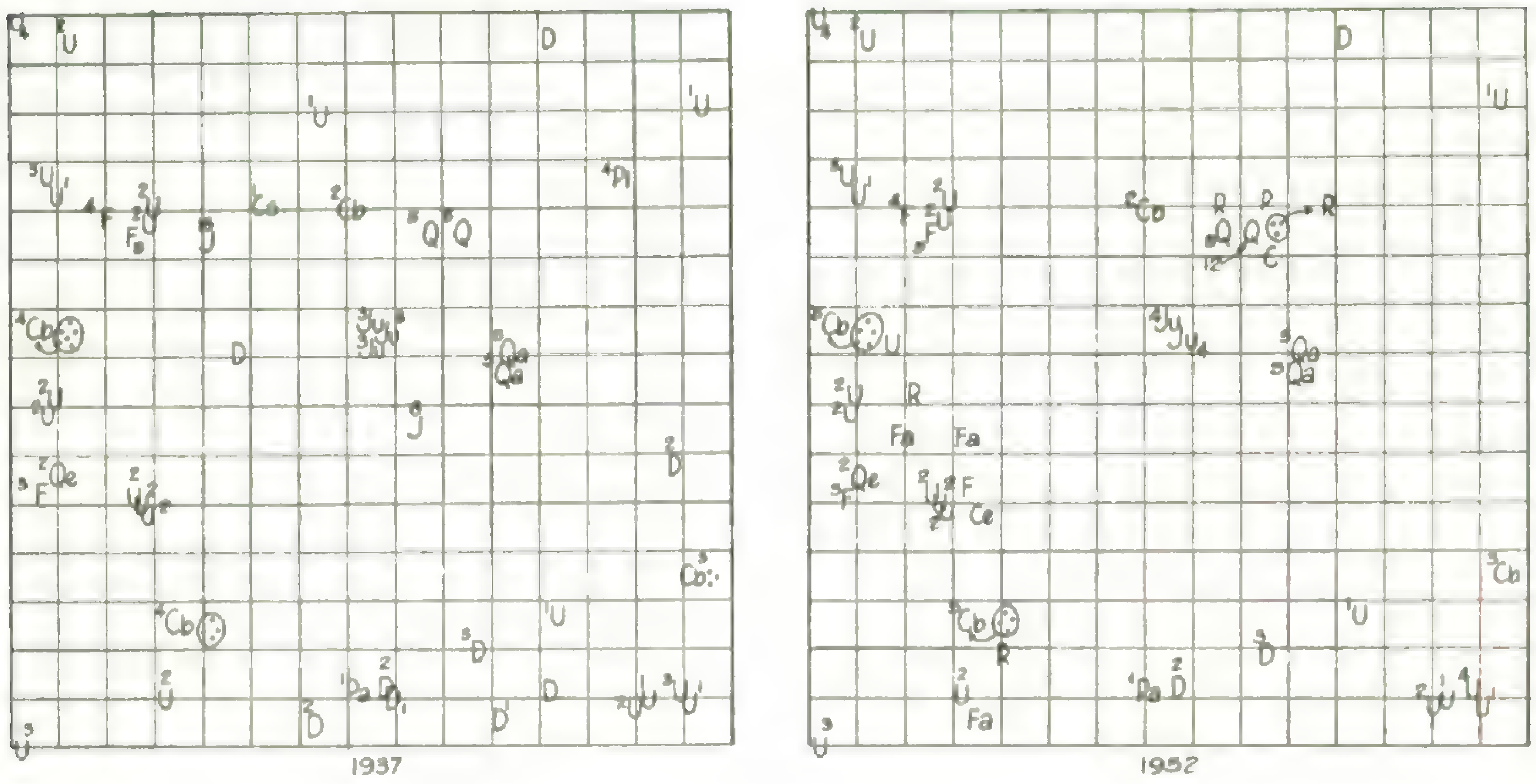

Fig. 1. Plots of a quadrat in the Oak Coppice Association for 1937 and 1952: Q = *Quercus alba*, C = *Carya ovata*, Cb = *Carya tomentosa*, Ca = *Cercis canadensis*, Co = *Cornus asperifolia*, D = *Diospyros virginiana*, F = *Fraxinus americana*, Fa = *Fraxinus quadrangulata*, J = *Juniperus virginiana*, Ju = *Juglans nigra*, P = *Prunus serotina*, Pa = *Prunus* sp., Pl = *Platanus occidentalis*, Qa = *Quercus imbricaria*, Qe = *Quercus velutina*, R = *Rhamnus caroliniana*, U = *Ulmus fulva*. Numerals indicate approximate diameter (DBH) to nearest inch.

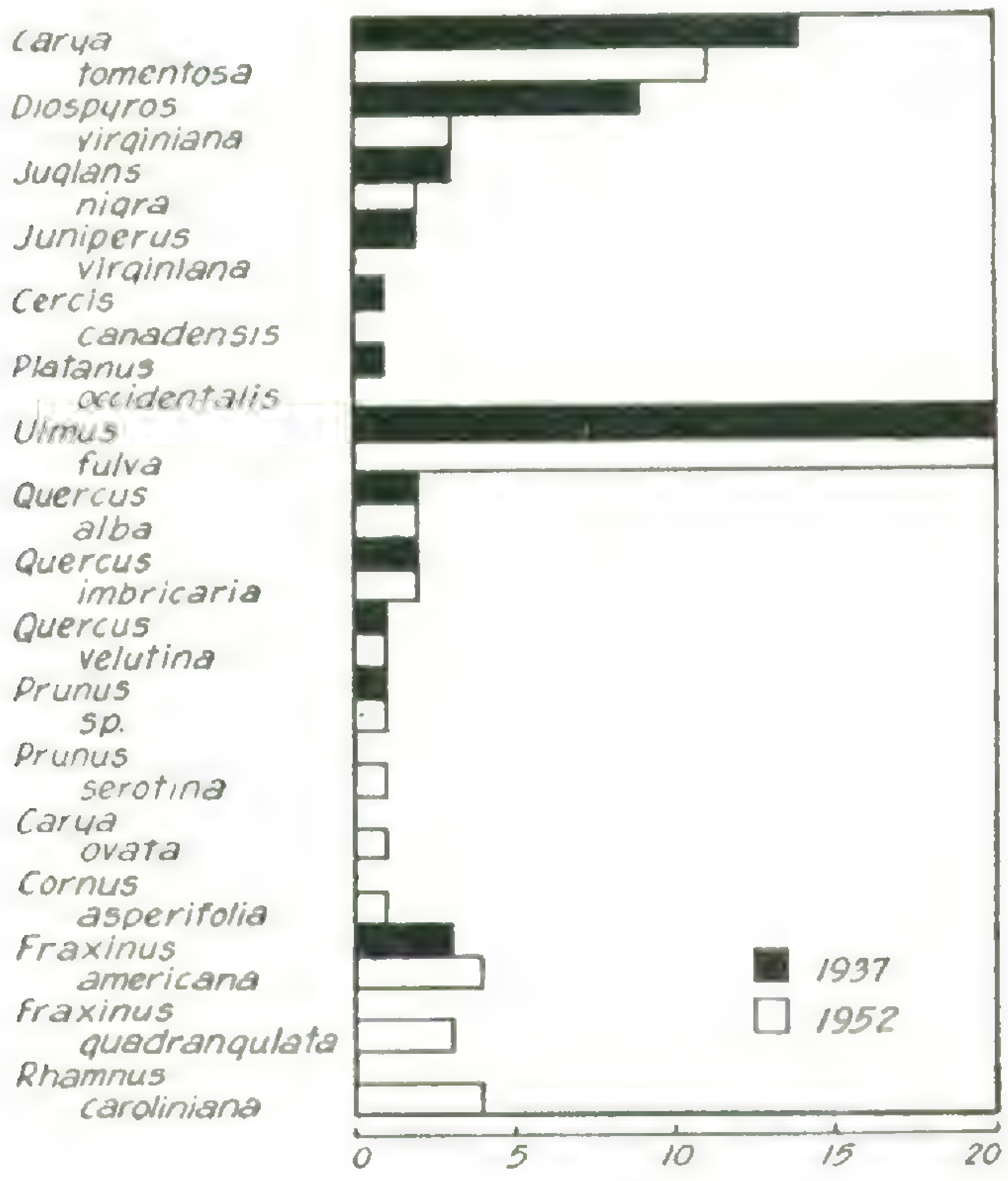

Fig. 2. Diagram representing relative numbers of plants of the species on a quadrat in the Oak Coppice Association in 1937 and 1952.

Recent inspection of the quadrat has revealed a great change in the growth habit of the forest trees. Now the White and Shingle Oaks, Mocker-nut Hickory, and Black Walnut have lost their lower limbs, their trunks are clean twelve to fourteen feet above the ground, and their crowns have developed more spread. The White Oak is still the dominant tree and has made considerable growth. Plants demanding large amounts of light, such as Redbud, Red Cedar, and Persimmon, have mostly been "shaded" out. At least one-fourth of the Persimmons have died and those remaining are in poor condition. The Slippery Elms are no less numerous, but the trees have grown very little. Some seedlings of Shagbark Hickory *(Carya ovata)*, White Ash *(Fraxinus americana)*, Blue Ash *(Fraxinus quadrangulata)*, Black Cherry *(Prunus serotina)*, and Rough-leaved Dogwood *(Cornus asperifolia)* have recently become established in the quadrat.

The record of this quadrat shows how quickly the forest species may become dominant and destroy an "open" aspect. The early land-use history of this area is not clear. It is believed that it had been pastured, and the numerous stump sprouts indicate that some pole-wood had been cut. Pasturing and the cutting of pole-wood promoted the rapid growth of light-loving plants such as Red Cedar, Redbud, and Persimmon, which formed a conspicuous part of the woody growth at the time of the first mapping of the quadrat. Since then and following a more conservative land-use program in which the area has not been pastured or burned, the forest trees have grown so vigorously as to dominate the quadrat area and "shade out" the light-loving plants. The many Slippery Elms, Persimmons, and

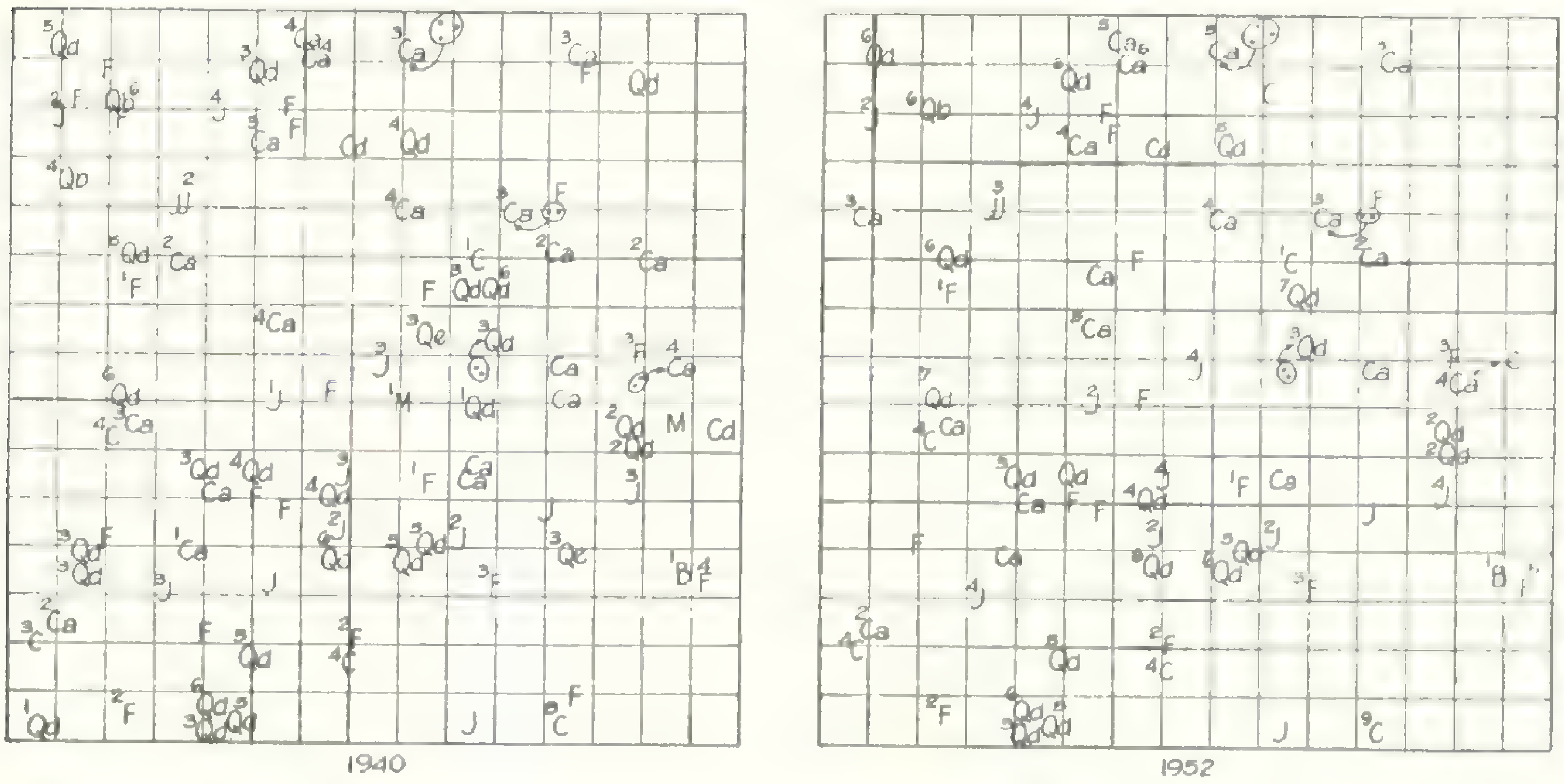

Fig. 3. Plots of a quadrat in the Oak-Hickory Association for 1940 and 1952: Am = *Amelanchier canadensis*, C = *Carya ovata*, Ca = *Carya Buckleyi*, Ce = *Celtis pumila*, F = *Fraxinus americana*, J = *Juniperus virginiana*, M = *Morus rubra*, Qb = *Quercus marilandica*, Qd = *Quercus stellata*, Qe = *Quercus velutina*.

Numerals indicate approximate diameter (DBH) to nearest inch.

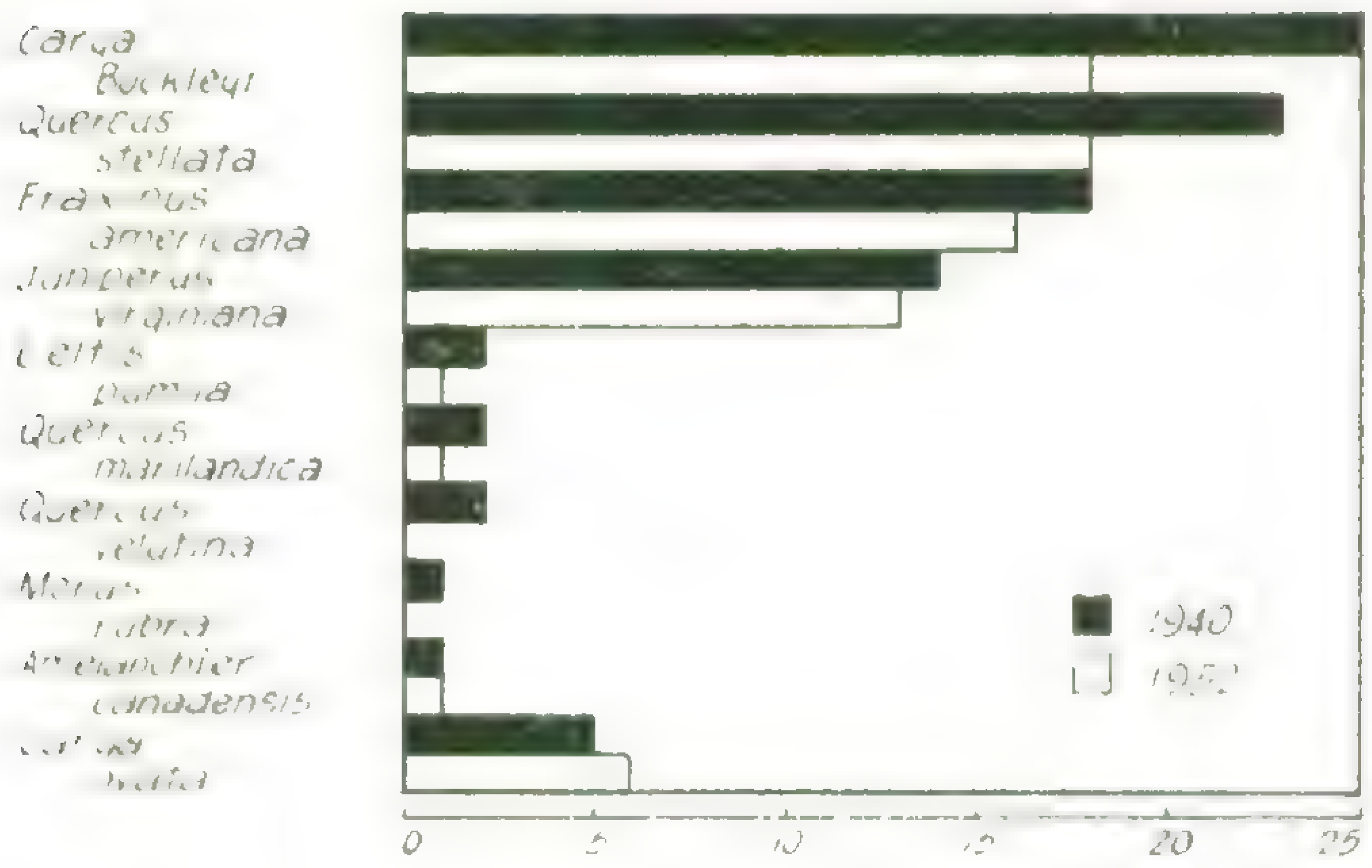

Fig. 4. Diagram representing relative number of plants of the species present on a quadrat in the Oak-Hickory Association in 1940 and 1952.

the Sycamore apparently germinated in the quadrat area about 1924 when it was set aside as a forest preserve. The grassy and otherwise herbaceous ground cover, so conspicuous at the time of the first mapping, has been replaced with duff of forest litter in which seedlings of Shagbark Hickory, White and Blue Ash, Indian Cherry, and Rough-leaved Dogwood have become established.

Quadrat in the Oak-Hickory (Quercus stellata-Carya Buckleyi) Association.—This quadrat (figs. 3 and 4) had been established in an oak-hickory forest just above a glade area. Here the Union Silt Loam overlays a somewhat massive phase of the Cotter Formation of dolomitic limestone. The early map shows small Post Oaks *(Quercus stellata)* and Pignut Hickory *(Carya Buckleyi)* as the dominant trees, and the Red Cedar *(Juniperus virginiana)* and White Ash *(Fraxinus americana)* were also numerous. Other species are mostly represented by seedlings.

The recent map indicates the continued dominance of the Post Oak and Pignut Hickory, but some of these trees have been lost in a natural thinning process. Many of the seedling trees have been lost, along with two large Black Oaks *(Quercus velutina)* and a Black Jack Oak *(Quercus marilandica)*.

The greater numbers of Red Cedar and the numerous seedlings on the early map indicate that more light entered the quadrat twelve years ago. This "open" aspect favored a lower branching habit of all the trees. Now the Post Oak and Pignut Hickory have made considerable growth and support well-developed crowns. They have lost many of their lower branches. Such a closing of the crown canopy has "shaded out" some of the Red Cedars and many seedlings of other trees.

Quadrat in the White Oak-Sugar Maple (Quercus alba-Acer saccharum) Association.—This quadrat (figs. 5 and 6) is located on a lower slope with a western exposure. The soil is the Union Silt Loam overlaying the basal sandstone phase of the Cotter Formation of rocks. The early map shows the White Oak as the dominant tree. The Sugar Maples, though not as large, were then of sufficient

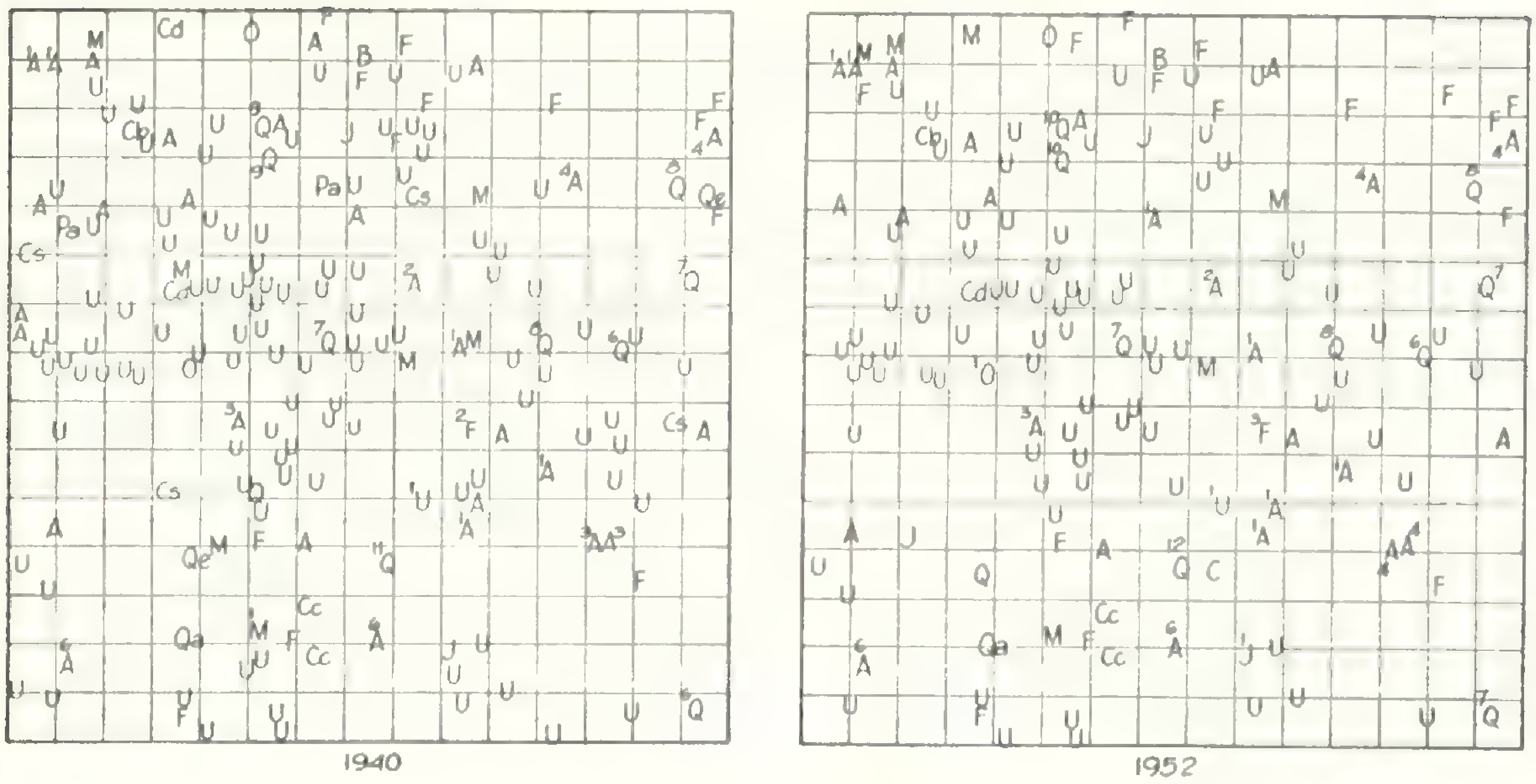

Fig. 5. Plots of a quadrat in the White Oak-Sugar Maple Association for 1940 and 1952: A = *Acer saccharum*, B = *Bumelia lanuginosa*, Cb = *Carya tomentosa*, Cd = *Celtis pumila*, Cs = *Cercis canadensis*, F = *Fraxinus americana*, J = *Juniperus virginiana*, M = *Morus rubra*, O = *Ostrya virginiana*, Pa = *Prunus* sp., Q = *Quercus alba*, Qu = *Quercus velutina*, U = *Ulmus fulva*.

Numerals indicate approximate trunk diameters (DBH) to the nearest inch.

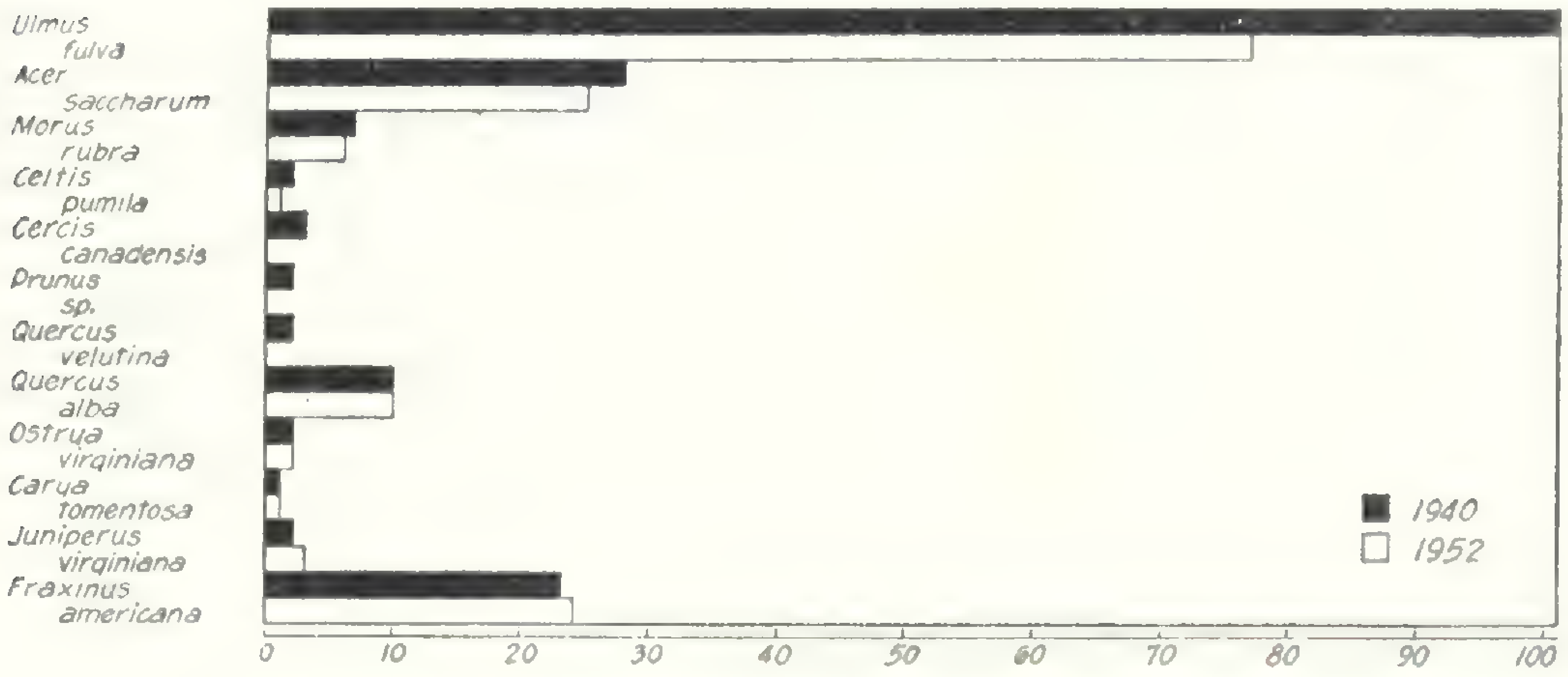

Fig. 6. Diagram representing relative numbers of plants of the species present on a quadrat in the White Oak-Sugar Maple Association.

size and vigor to suggest their co-dominance with the White Oaks. As shown in figs. 5 and 6, the seedlings of Slippery Elm *(Ulmus fulva)* were conspicuous at that time. It is also apparent that there was enough light entering the area to support several Redbuds *(Cercis canadensis)*, as well as Red Cedar *(Juniperus virginiana)*, Dwarf Hackberry *(Celtis pumila)*, and Red Mulberry *(Morus rubra)*. A single Hop-Hornbeam *(Ostrya virginiana)* was thriving.

Recent inspection of the quadrat shows that the White Oak continues to be dominant and that the trees have made appreciable growth. The Sugar Maple is growing slowly and is being suppressed by the White Oak. At least 20 per cent of the Slippery Elm seedlings have been lost and those remaining have made no

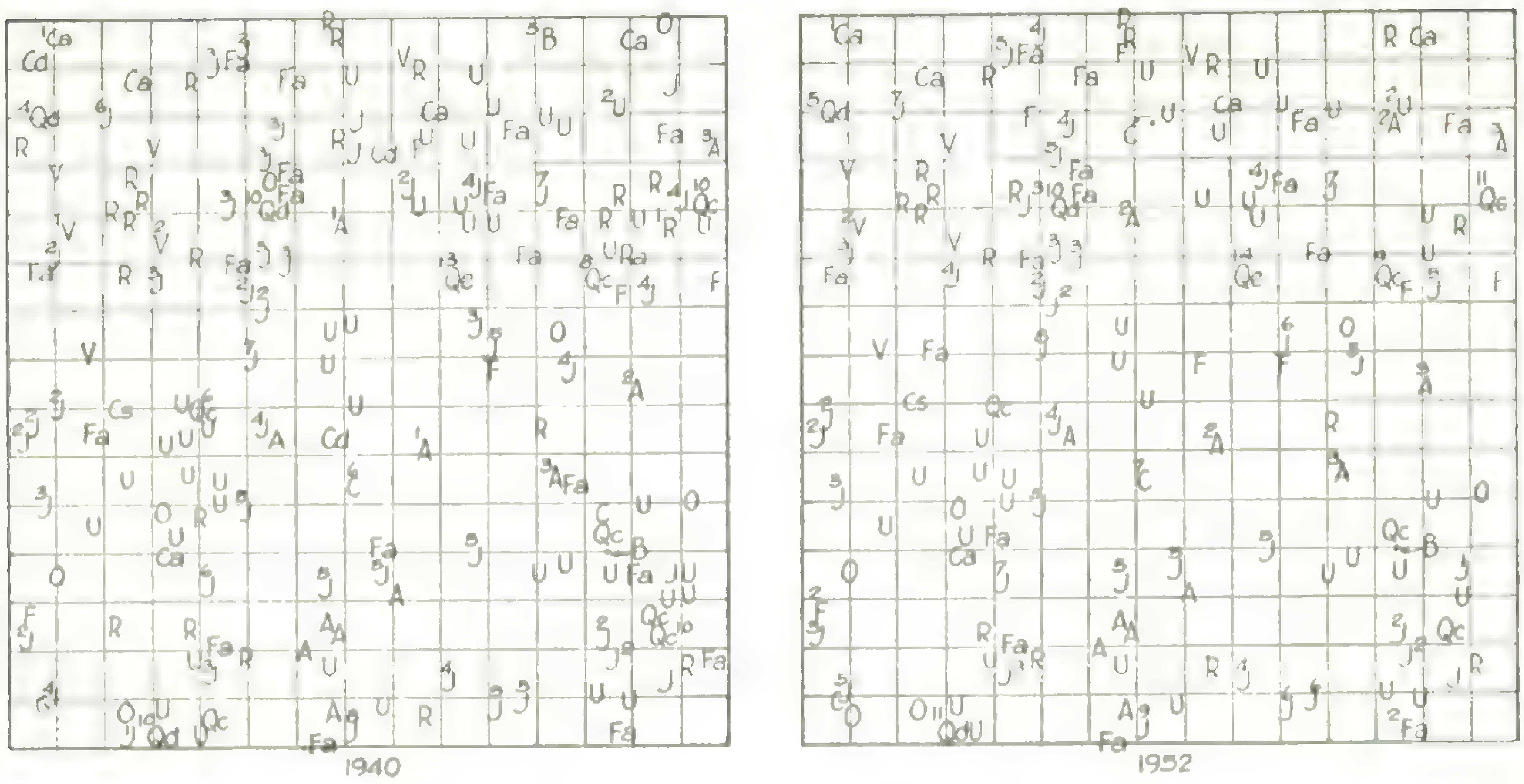

Fig. 7. Plots of a quadrat in the Red Cedar-Chinquapin Association for 1940 and 1952: A = *Acer saccharum*, Am = *Amelanchier canadensis*, B = *Bumelia lanuginosa*, C = *Carya ovata*, Ca = *Carya Buckleyi*, Cd = *Celtis pumila*, F = *Fraxinus americana*, Fa = *Fraxinus quadrangulata*, J = *Juniperus virginiana*, O = *Ostrya virginiana*, Qc = *Quercus Muhlenbergi*, Qd = *Quercus stellata*, Qe = *Quercus velutina*, R = *Rhamnus caroliniana*, Ra = *Rhamnus lanceolata*, U = *Ulmus fulva*, V = *Viburnum rufidulum*.

Numerals indicate approximate trunk diameters (DBH) to the nearest inch.

noticeable growth. The Redbud, Red Mulberry, and Dwarf Hackberry have suffered from reduced light brought about by the expanding crowns of the White Oaks. Red Cedars, though as frequent, have made but little growth and are in poor condition.

The occurrence of old stumps in the area about the quadrat indicates that some trees had been cut prior to the first mapping. Such cutting probably permitted the entrance of enough light to encourage growth of Redbud, Mulberry, Dwarf Hackberry, Red Cedar, and the many seedlings of Slippery Elm. It also may have brought about increased growth of the remaining White Oaks which have become entirely dominant at the expense of the Sugar Maples and seedling trees.

Quadrat in the Red Cedar-Chinquapin Oak (Juniperus virginiana-Quercus Muhlenbergi) Association.—This quadrat (figs. 7 and 8) is located on a lower slope with a western exposure. The soil is very shallow and lies immediately upon the somewhat massive phase of the Cotter Formation of rock. The early map shows a considerable number of Red Cedars 4–7 inches in diameter and a number of Chinquapin Oaks of comparable size. These two species were the dominant trees of the quadrat. Also present were two large Post Oaks *(Quercus stellata)*, a Black Oak *(Quercus velutina)*, and a single large Chittimwood *(Bumelia lanuginosa)*. At that time the quadrat had a "brushy aspect", with Slippery Elm *(Ulmus fulva)* making the greater part of the undergrowth, and in less abundance Redbud *(Cercis canadensis)*, Indian Cherry *(Rhamnus caroliniana)*, Hop-Hornbeam *(Ostrya virginiana)*, Dwarf Hackberry *(Celtis pumila)*, Lance-leaved Buckthorn *(Rhamnus lanceolata)*, Shadbush *(Amelanchier canadensis)*, and Black Haw

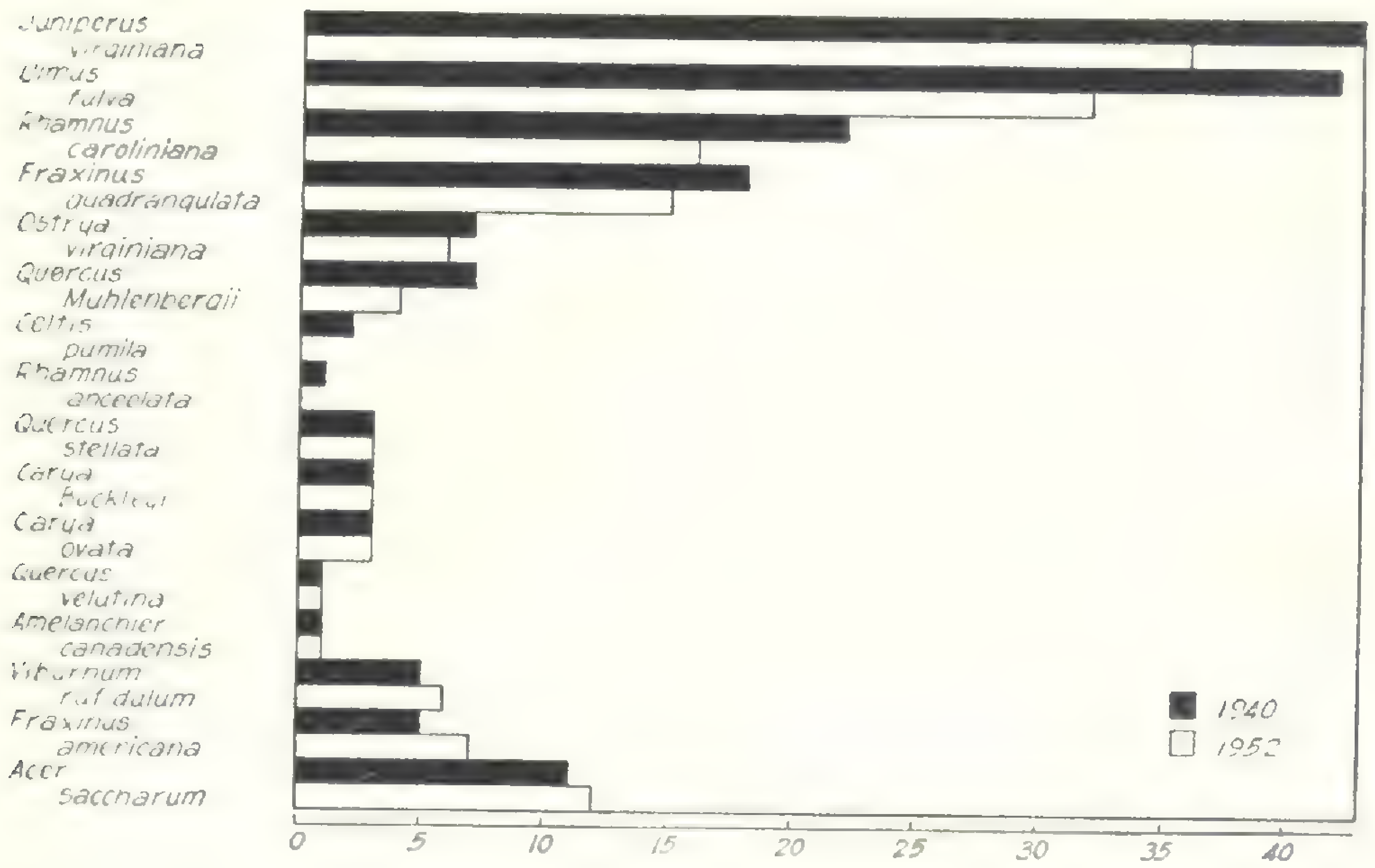

Fig. 8. Diagram representing relative numbers of plants of the species present on a quadrat in the Red Cedar-Chinquapin Oak Association for 1940 and 1952.

(Viburnum rufidulum). There were also seedlings of Blue Ash *(Fraxinus quadrangulata)*, White Ash *(F. americana)*, and small trees of Sugar Maple *(Acer saccharum)*.

The recent survey of the quadrat shows that about one-sixth of the Red Cedar trees were lost through competition and that the ones left had grown considerably. Some Chinquapin Oaks had also died but the remaining trees had made some growth. There was no change in the number of oaks and hickories and they also have grown. The single large Chittimwood has died. The greatest change is in the understory growth. Almost a fourth of the Slippery Elms have died and those left have scarcely grown either in diameter or height. Other understory trees as Indian Cherry and Hop-Hornbeam are less frequent but are growing vigorously. Lance-leaved Buckthorn and Dwarf Hackberry have died. There are a few more trees of Shadbush and Black Haw and they are thriving. The number of White Ash and Sugar Maple trees has increased slightly, but their seedlings and small trees are growing slowly. The Blue Ash, present mostly as small and seedling trees, has decreased in number, although the plants remaining are making moderate growth.

On this and the preceding quadrats, many specimens of Slippery Elm, White Ash, Red Cedar, Post Oak, Pignut Hickory, and Sugar Maple are only 4–5 feet in height. On casual inspection they give the appearance of young plants but actually they are 15–20 years old.

OBSERVATIONS ON FOREST SUCCESSION

Time-lapse studies presented in the foregoing forest quadrats and in the more general association maps in an earlier paper[3] have revealed significant facts concerning forest succession for the area under consideration. The conclusions reached for the local area may have a wider application for the Ozark region in general. One of the outstanding features brought out by this study has been the marked inability of most species to invade established associations except in the event of a catastrophe such as fire, lumbering, heavy pasturage, or abrupt changes in climate of considerable duration.

In the four quadrats described the invasion and decline of numerous seedlings have been observed. With almost no exceptions species have been able to invade established associations and to demonstrate vigor sufficient to suggest the possibility of their offering serious competition to established trees. It was found that the greater number of seedlings of species mentioned in the foregoing quadrat reports originated in the years following a major catastrophe, in this case the drought period of 1930–1936, which seriously weakened the trees in the region of the Arboretum Forest Preserve. During the time lapse of this study it has been observed that the existing associations continue in their "catastatic" state. Historical data indicate that a catastrophe will incite germination of seeds and start successful invasion of the disturbed association.

In any event, the association will be a happenstance entirely dependent upon the kind of seed immediately available and the peculiar requirements both for germination and survival of the seedlings. Even though the seedlings may survive and reach maturity they may not represent the best-adapted species for the site. However, no other species with similar requirements for germination were present at the time that the site was a frontier ready for invasion. Those plants surviving to seed-producing maturity will then become conspicuous in the forest association. It is believed that such species may often so completely occupy the site, filling shallow soils with roots and shading the soil surface with their tops, as to prohibit or retard seedling growth. The invasion of new plants in this established local association is thus prevented, and the association may be perpetuated for many generations and cover considerable areas. Plants unsuited for a particular site are often short-lived, as illustrated by the many forest trees used in landscape planting which mature early and become an easy victim of minor accidents. If the association is weakened, it will be vulnerable to seedling invasion. Better-adapted species may then enter if seed sources are adequate, or, lacking this condition, the growth of seedlings will comprise a regeneration of the existing association.

The Blue Ash *(Fraxinus quadrangulata)* has offered an excellent opportunity to study invasion as related to seed source. The early history of the area has shown that many Blue Ash trees had been cut for fire-wood and for farm-implement manufacture. When the Forest Preserve was established there were few trees of Blue Ash. Almost no seedlings were to be found in the Forest Preserve, but now many Blue Ash trees are fruiting abundantly, and the seedlings are invading adjacent open areas.

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[3] Beilmann and Brenner, op. cit.

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Volume XXXIX Number 3

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PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price	$10.00 per volume
Single Numbers	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Annals
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Vol. 39 SEPTEMBER, 1952 No. 3

ARTHROXYLON, A REDEFINED GENUS OF CALAMITE*

FREDDA D. REED**

During the investigation of a specimen of a calamitean stem from an American coal field (described below) its relationship to *Arthrodendron* Scott 1899 (*Calamopitus* Will. 1871) was discovered. However, the name *Arthrodendron* may not be employed now, because, as will be shown, it is invalid in this sense.

In his first accounts of this material Williamson (1871, 1871a) was convinced of: (1) the calamitean affinity of the specimens; and (2) the fact that they differed structurally from other calamitean stems with cellular preservation that had been described. Accordingly, he called the specimens *Calamopitus.* But as for a binary name, he wrote: "I am disposed to regard all specific names and definitions as worthless. They separate things that I believe to be identical, and confound others that are obviously distinct" (1871). After some consideration of the different structural types of calamitean stems, that is *Calamodendron* Brong. 1849, *Arthropitys* Goepp. 1864, and *Calamopitus* Will. 1871, Williamson and Scott (1894) concluded: "We think . . . . *Calamopitus* should be retained. Besides the peculiar structure of its medullary rays it is characterized by the predominance of reticulated elements in its wood."

Sometime later Seward (1898) explained the substitution of the term *Arthrodendron* for *Calamopitus* thus: "Williamson's name *Calamopitys*[1] had previously been made use of by Unger for plants which do not belong to the Calamarieae. As it is convenient to have some term to apply to such stems as those which Williamson made the type of *Calamopitys,* the name *Arthrodendron* is suggested by my friend Dr. Scott as a substitute for Williamson's genus." Farther along, Seward 1898) recognized and elaborated on the three structural types, or "sub-genera" as he called them, yet while he mentioned various species of both *Calamodendron* and *Arthropitys* there was no binomial for *Arthrodendron.*

[1] Seward here uses the orthographic form.

* This investigation was aided by grants from the Bache Fund of the National Academy of Science and from the Penrose Fund of the American Philosophical Society. The author also wishes to express thanks to members of the geology staff of the British Museum of Natural History, especially to Mr. F. M. Wonnocott, for the loan of parts of the Williamson Collection.

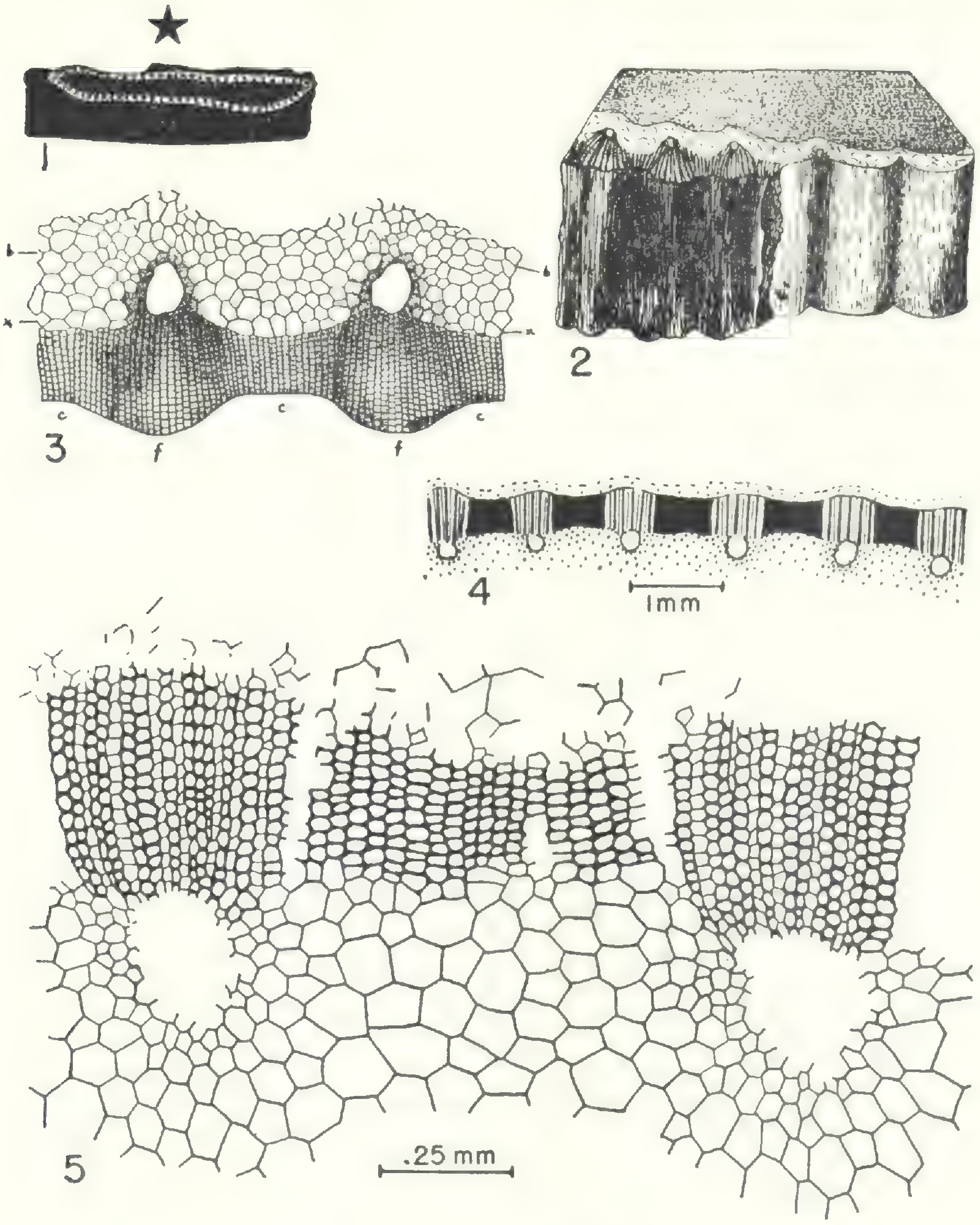
** Mount Holyoke College, South Hadley, Mass.

Since that time authors, as Zeiller (1900), Jongmans (1915), Leclercq (1925), Hirmer (1927), Hofmann (1934), Knoell (1935), Emberger (1944), and Arnold (1947) have employed Seward's terminology for calamitean stems with structure preserved. In the meantime, while the term *Arthrodendron* was dangling without a proper description or without having been typified, Ulrich (1910) described some fossil fucoid plants which were found near Kadiak, Alaska, to which he gave the name *Arthrodendron diffusum* gen. et sp. nov.

The term *Arthrodendron* seems more appropriate for a calamite than for an alga of uncertain affinity; also, it has been widely used in the former sense, for it is to be found in all the text-books of paleobotany. Nevertheless, there is no denying the valid priority of *Arthrodendron diffusum* Ulrich (1910), and therefore, I propose the name *Arthroxylon* for calamitean stems of this type.

Because of the historical significance and classical value, as well as the quality and quantity of the preparations of Williamson's specimens, it seemed appropriate that his material be redefined and given a binary name thereby making it the type material for *Arthroxylon*. In order to do so it was necessary to examine the preparations; hence, negotiations were completed with the British Museum of Natural History for the loan of the Williamson Collection of slides of calamites which he called *Calamopitus*. The collection received consisted of 21 preparations in two series, made from two different stems from different localities. In each series there are transverse and longitudinal—both radial and tangential—sections of the stems. Williamson described and figured these two calamitean stems in different articles (Williamson 1871, '71a); the stem of series 52–60 bears the earlier publication date.

A comparison of comparable or homologous sections of the two series, that is, transverse with transverse and tangential with tangential, leaves one with the impression that, although the two stems seem to be essentially similar in type and distribution of cells and tissues, they appear to be fundamentally quite different. As these stems also are patently of different ages, one having more than four times as much secondary wood as the other, the possibilities should be considered: (1) that their differences are more apparent than real because of disparity in age and size; (2) of their being stems of different orders, that is, primary or secondary axes from plants of the same species and consequently of a somewhat different structure; or (3), that the two stems actually are from different species. The first possibility may be rejected because of fundamental differences in cellular structure of the first formed and comparable secondary elements. As to their being stems of different orders—that remains a possibility, for as yet we do not know the range of structural variability of stems of different orders of the calamites so as to be able to say whether one is primary axis and another a lateral branch on the basis of isolated fragments. However, on the basis of primary structure it would seem most expedient, for the present at least, to recognize the two stem fragments as different species of *Arthroxylon*. The stem of series 35–46 is here designated *Arthroxylon Williamsonii*, and the other, series 52–60, *Arthroxylon oldhamium*.



Figs. 1–5. *Arthroxylon Williamsonii*

Fig. 1. Transverse section (about natural size) of a thin-walled *Arthroxylon (Calamopitus)*, imbedded in its dark matrix. Fig. 2. Small portion from opposite the star in fig. 1, viewed diagonally. Fig. 3. Small segment of fig. 1: b, pith cells; x, crenulated outline separating the pith from the persistent woody zone; c, primary medullary rays; f, woody wedges; after Williamson (1871). Fig. 4. Diagram of portion of transverse section of stem (Will. Coll. No. 35). Fig. 5. Detail of portion of transection (Will. Coll. No. 36).

The following brief description of the two species is intended to be supplementary to the original accounts (Williamson 1871, 1871a). While nine of the sections of series 35–46 and six of series 52–60 are longitudinal through nodal regions, yet because of the methods of preparation the orientation of the plane was more or less randomized. For accurate reconstruction of the node, carefully oriented serial cuts are necessary; hence, the sections at hand are inadequate for a detailed description of the nodal region. The nodal region unquestionably is im-

portant and may yet yield further diagnostic characters; moreover, it has not been ignored in the broader phases of this investigation. However, in the present report the internodal region is the only portion considered, since the great bulk of available preparations, or those made in the future, are likely to be of this region. Furthermore, the internodal region does provide diagnostic criteria, and attention is focused on those features which reveal characters thought to be specific in nature.

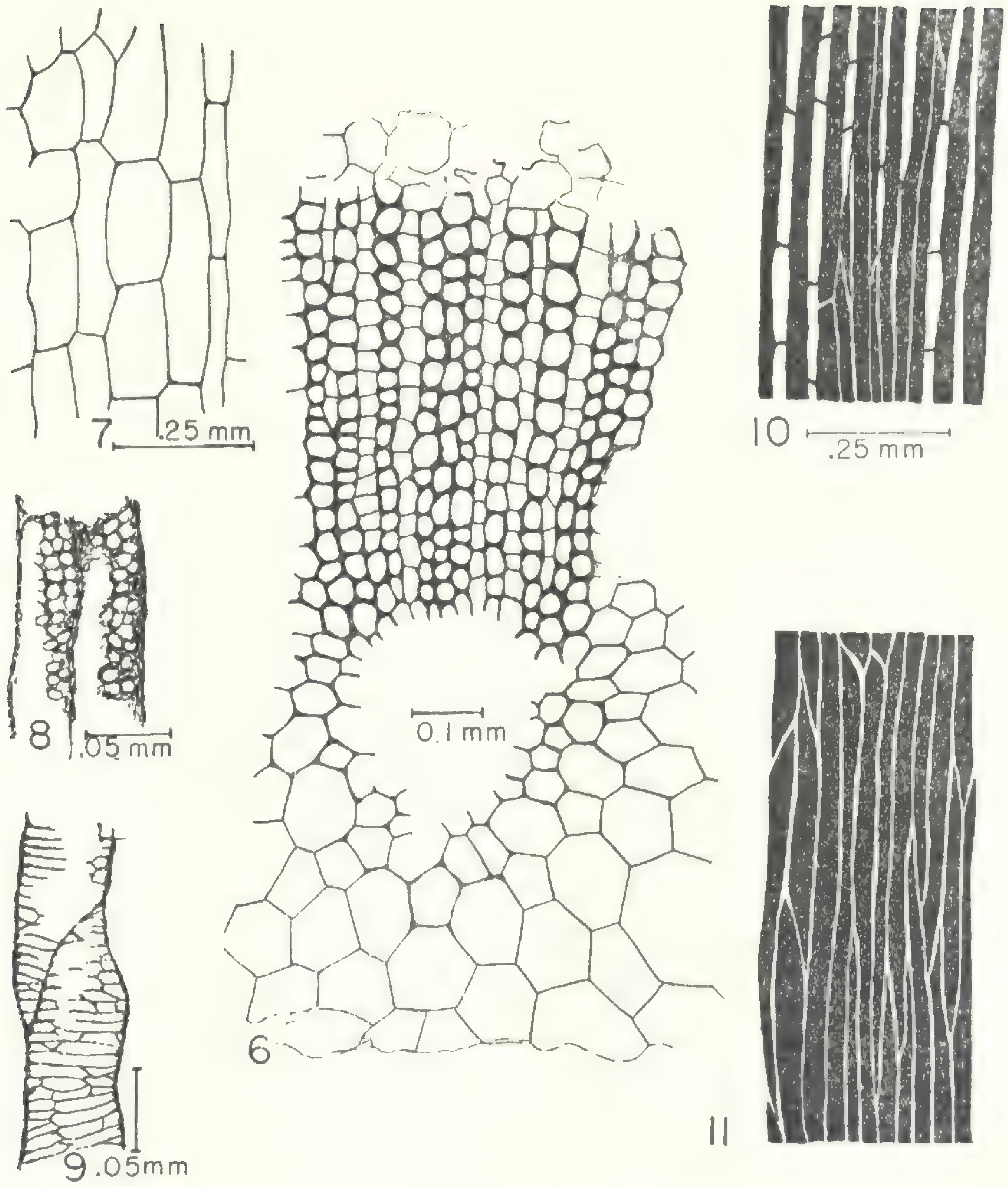
Arthroxylon Williamsonii

This account is based upon twelve preparations (Will. Coll. 35–46) made from a portion of a decorticated stem. Except for the title, "On the Organization of the fossil plants of the Coal-Measures" there is no information in Williamson's article (1871a) as to the origin of this particular specimen. He simply introduced it by saying: "I have next to call attention to a peculiar form identical in many respects with one that I described in the fourth volume of the third series of the Memoirs of the Literary and Philosophical Society of Manchester and to which I gave the generic name *Calamopitus*." The stem measured about 3 cm. in diameter; of this diameter the larger part by far is that of the fistular pith area, for the woody cylinder is only about 0.4 mm. thick (figs. 1, 2).

The thin-walled pith cells are sharply delimited from the secondary elements both in transverse and longitudinal views (figs. 3, 4, 5, 7). The carinal canals, conspicuous because of their relatively large size, appear to have been formed by the disintegration of both protoxylem and metaxylem. The exact number of canals was not determined, for neither of the transverse sections is entire; it was possible to count more than sixty, and the number probably would not exceed seventy. Williamson's figure 19 (fig. 1), which doubtless was made before the material was sectioned, shows 67 canals. Radiating from the canals are 14–17 rows, expanding to 18–20 at the periphery of the woody cylinder, of secondary conducting tissue averaging about 16 layers deep (figs. 4, 5, 6). These are composed of rows of tracheids with interspersed rows of parenchyma. There is some variation in the ratio of the number of rows of the former to the latter but it is usually two to one (figs. 5, 6). The rows of parenchyma—Williamson's "secondary rays"—are not easily distinguishable from the tracheids in transection, but in tangential section they stand out by virtue of their thinner walls and their lesser length (fig. 10).

The markings of the tracheids, which are scalariform to reticulated, are found chiefly, but not altogether, on the radial walls (figs. 8, 9).

The elements of the interfascicular secondary tissue—the "primary medullary ray" of Williamson—are organized in 16–18 radial rows (fig. 5), which are as regularly disposed as are the rows of the fascicular tissue. In transection the dimensions and thickness of the cell walls do not differ greatly from those of the tracheids. These features, that is, disposition, size, and thickness of the walls, combine to make the area appear extraordinarily like the fascicular area. However, upon closer observation some differences become apparent: (1) there is an



Figs. 6–11. *Arthroxylon Williamsonii*

Fig. 6. Detail of woody wedge (Will. Coll. No. 36). Fig. 7. Longitudinal section of portion of pith bordering canal—canal to the right (Will. Coll. No. 44). Fig. 8. Longitudinal radial walls of tracheids of X^2 (Will. Coll. No. 40). Fig. 9. Longitudinal walls of tracheids in vicinity of node (Will. Coll. No. 41). Fig. 10. Longitudinal tangential section of tracheids (shaded) and parenchyma (Will. Coll. No. 37). Fig. 11. Tangential longitudinal section through interfascicular area (Will. Coll. No. 37).

absence of rows of thin-walled parenchyma cells among the rows of thick-walled cells as were found among the rows of tracheids; and (2) in longitudinal section (fig. 11) the thick-walled cells are not only devoid of scalariform and reticulated markings but they are shorter than the tracheids and have a fusiform appearance. In short, these thick-walled fibrous cells appear to have been derived from fusiform

cambial cells and to have matured without further elongation and without the development of specialized secondary thickenings as occurred in the maturation of the tracheids, or without subsequent transverse divisions of fusiform initials as in the formation of the wood parenchyma.

As is shown in figs. 5 and 6, there is some preservation exterior to the woody cylinder. The preservation of this region is so slight as to make description impossible; nevertheless, its presence does clearly show the limitation of the secondary wood.

Arthroxylon oldhamium

Although Williamson's description of the two specimens of *Arthroxylon oldhamium* appeared in 1871 it was not until much later (1896) that he wrote of their origin and their coming into his possession. His account is as follows:

> Early in the fifties when I was commencing in an unsystematic way to grind down fragments of various objects for microscopic investigations, I found in a drawer of my cabinet a portion of a Calamite that had been extracted from one of the ironstone nodules of the coal measures. I was not at that time provided with a lathe or any other sort of cutting or grinding machinery; but as the calamite presented indications that some structure might be found in it, I chipped off with hammer and chisel such fragments as appeared suitable, and ground them down on a flagstone, obtaining nine curious sections, showing the structure of a woody zone where it was in immediate contact with the medulla.
>
> Having then no intention of making any special use of these preparations, they were put away in a drawer of the cabinet and almost forgotten.
>
> About the same time I had instructed a working joiner to fit up for me a small horizontal grinding wheel, worked by a pedal, and which was not complete. Somehow this little transaction gave the joiner the idea that I was interested in stones; and one evening he called upon me, bringing in his apron a number of rough fragments of sandstone. He had been working at a stone quarry near Oldham, and had picked up from the refuse of the quarry a basketful of stones which appeared new to him, and he concluded that they might be interesting to me. They were in the main the merest rubbish, but amongst them I detected a fragment which was equally elegant and remarkable. How it had escaped destruction from the unprotected way in which it had travelled in such rough company was to me an absolute mystery. The specimen looked like the base of one calamite within the interior of a single joint of another and much larger one; but at that time I was wholly unable to construct any reasonable hypothesis explaining how the two parts had been brought into mutual relationship.
>
> In later days, when the specimen so oddly and accidentally obtained, came to be intelligently studied, its history became clear enough, and the priceless fragment is now one of the most precious gems in my cabinet. Some time after the occurrence of the above event Sir Charles Lyell happened to be at my home, and I showed him this specimen. He was much struck with its interest and novelty, and asked me to allow him to publish a figure of it in the fifth edition of his "Manual of Elementary Geology", upon the preparation of which he was engaged. Of course I consented, and the figure appeared in 1855 on page 368 of that work . . . .[2]

The "nine curious sections" referred to in the above quotation are the sections of Will. Coll. series 52–60. On these slides there are such small pieces of plant material that were it not for Williamson's figures (1871, fig. 2) showing its appearance before being sectioned, its calamitean affinity might be argued.

Preservation of this stem is limited to a very small portion of the secondary woody cylinder. Figure 12, a diagram from the better of the two transverse sec-

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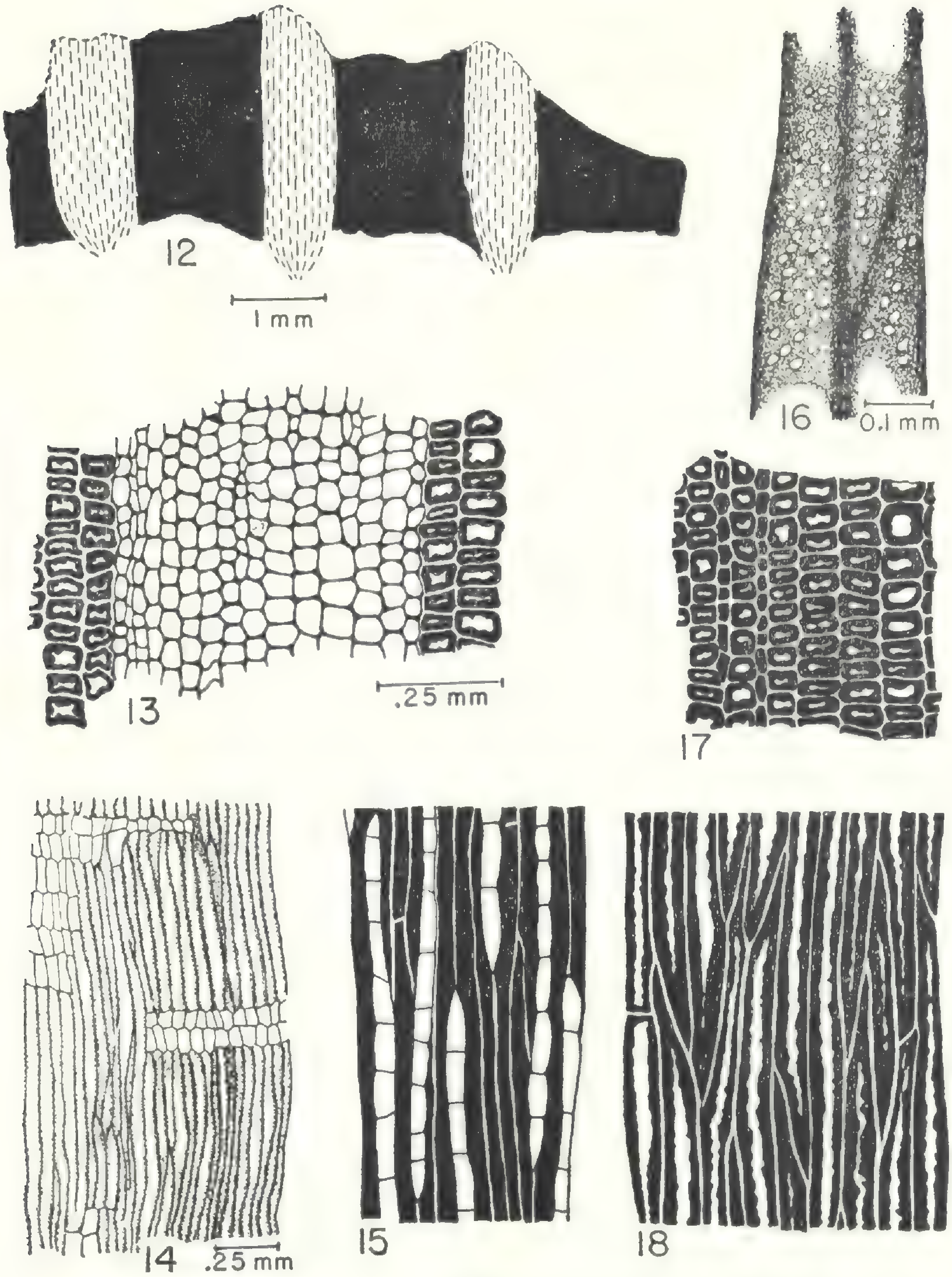
[2]The author wishes to express appreciation to Dr. H. N. Andrews for calling attention to the above quotation.



Figs. 12–18. *Arthroxylon oldhamium*

Fig. 12. Diagram of portion of transection of stem (Will. Coll. No. 52). Fig. 13. Detail of portion of fascicular wood bordered on either side by fibrous parenchyma (Will Coll. No. 52). Fig. 14. Longitudinal radial section through fascicular area (Will. Coll. No. 58). Fig. 15. Longitudinal tangential section through fascicular area (Will. Coll. No. 54). Fig. 16. Longitudinal radial walls of tracheids (Will. Coll. No. 58). Fig. 17. Transection of portion of interfascicular area (Will. Coll. No. 52). Fig. 18. Longitudinal tangential section through interfascicular area (Will. Coll. No. 54).

tions, shows the same pattern of rows of fascicular xylem alternating with rows of thick-walled fibrous cells as was found in the former species. It is in the cellular detail and in the proportion of tissues, rather than in tissue pattern, that *A. oldhamium* differs from *A. Williamsonii.*

In *A. oldhamium* there are fewer rows composing a fascicular xylem area; there had not occurred as many anticlinal divisions of tracheid and wood parenchyma initials to increase the number of rows, with the result that in transection the xylem bands maintain approximately the same width from the early formed secondary wood to the peripheral region, that is, in so far as the tissue of the woody cylinder is preserved (fig. 12). As in *A. Williamsonii*, these bands are composed of rows of tracheids interspersed with rows of parenchyma, although in transection the elements of the two are indistinguishable in size and thickness of their walls (fig. 13). But, again, as in *A. Williamsonii*, the tangential sections show the pattern of distribution of parenchyma and tracheids, except that in *A. oldhamium* the parenchyma cells are proportionately shorter than in *A. Williamsonii* (fig. 15). The relative length of the tracheids and parenchyma cells is also shown in radial section (fig. 14). Despite the quality of the preservation of the cells of this stem the markings on the walls of the tracheids remain elusive, particularly in the internodal region; occasional views, as that of fig. 16, show a kind of reticulated pitting on the radial walls.

The interfascicular area (fig. 12) is markedly different in appearance from the corresponding area of *A. Williamsonii*, yet structurally the areas are essentially alike. In *A. oldhamium* the area is considerably more extensive, being composed of 30–35 rows as compared with 16–18 rows as in the former species. The elements are larger in transection, their radial and tangential dimensions are about $42 \times 65\ \mu$; they are vertically elongated, their length varying from four to ten times their width, with tapering end walls (figs. 17, 18).

These regularly disposed elements of the interfascicular area are rendered more striking by the simulated thickness of their walls (figs. 13, 17, 18). In his description of this tissue, Williamson wrote: "Each cell appears to have thick walls, like those of recent woody fiber, which I at first believed these tissues to be; but I think that the appearance in question is due to mineral infiltration, and that the true walls were thin." This opinion has been confirmed by examining the sections with a polarizing microscope. Instead of being so extremely thick-walled that the lumen of the cells was almost occluded, as they appear in ordinary transmitted light (figs. 13, 17), these fibrous cells were found to have been selectively infiltrated by a turbid carbonate (calcite) of fibrous habit. The carbonate formed pseudo-spherulite aggregates which show undulose or plumose extinction upon rotation of the object stage of the microscope.[3]

Arthroxylon Williamsonii from an American coal field.—

This stem fragment was found in a coal ball collected by the late Professor A. C. Noé from a strip mine near Petersburg, Indiana. In the Ditney Folio (1902) the coal of this locality is listed as Coal No. 5 of the Upper Carboniferous.

The coal ball was a relatively small one with dimensions of approximately $5 \times 6 \times 7$ centimeters. Like most of these calcareous nodules, it contained an

[3]The author is indebted to Dr. J. C. Haff of the Geology Department of Mount Holyoke College for the polariscopic determination of the mineral content of the cells.

assemblage of diverse plant remains—diverse in the number of genera represented as well as in the organs and tissues. The identifiable plant fragments, in addition to the calamitean stem, were roots and leaves of *Sphenophyllum*, *Lepidodendron* leaves, *Stigmaria* rootlets, some specimens of *Lepidocarpon,* a bit of tissue from a *Medullosa* petiole, scattered fern sporangia, and some synangia.

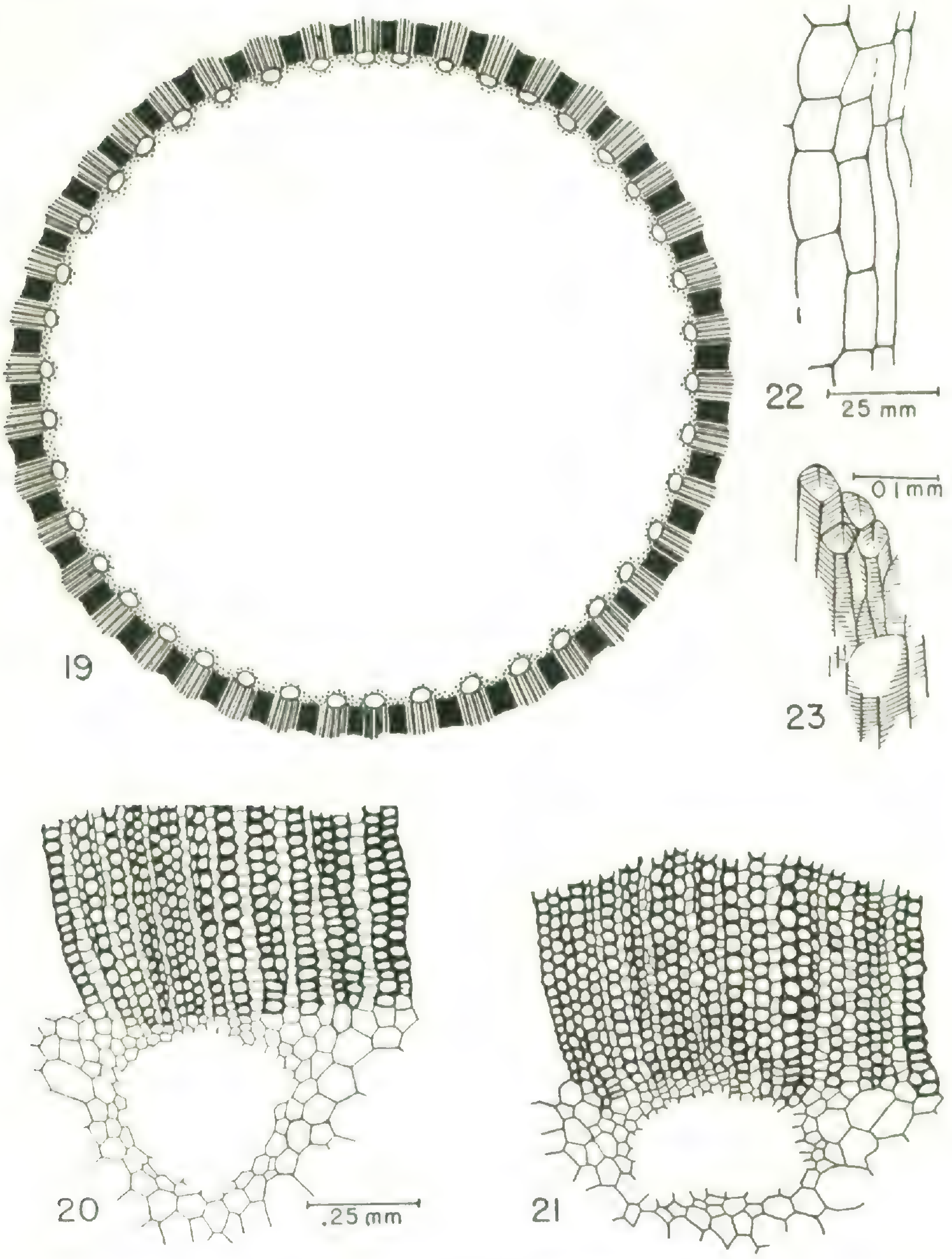
The following description of the specimen of *A. Williamsonii* is based upon 12 thin sections of the coal ball. They are labeled NR 1–12, and are deposited in the Museum of the Illinois State Geological Survey, Urbana, Illinois.

The calamitean material consisted of numerous pieces of wood which, while they were variously disposed and distributed throughout the width of the coal ball, seemed to lie in the same sedimentation plane. Also these pieces are comparable in structure and texture. Therefore, there seems but little doubt of their being parts of a stem that had been crushed and broken and the parts slightly separated before petrifaction. On this assumption all these woody fragments in section No. 5 were projected on paper, then the drawings were cut out and assembled in a ring; this assemblage provided the dimensions and proportions for the reconstruction shown in fig. 19. Preservation of the various tissues of this stem is far from complete, being limited to part of the pith, the elements of the woody cylinder, and occasional remnants of the cambium and phloem of the internodal region; also there seems to have been some chemical alteration of the cell walls which defaced the markings of the lignified cells, leaving the wall surface plain.

The Primary Tissues.—The thin-walled pith cells make a narrow peripheral zone which in transection rarely exceeds four cells deep (figs. 19, 20, 21). In transection the pith cells are roughly isodiametric; the innermost are the largest with an average diameter of about 80 μ, while the outer ones—those bordering the canal and the interfascicular secondary tissue—average about 30 μ in diameter. The cells are vertically elongated, the larger ones only slightly so, while the length of the smaller ones may exceed their width by ten or more times. All the pith cells have horizontal end walls (fig. 22).

There was a total of 42 carinal canals in the assembled pieces (fig. 19). Most of them seemed to have been formed by the complete breakdown of the primary xylem, yet in some instances, as in figs. 20, 21, 24, there are a few elements which, from their shape, position, and thickness of walls, seem to be of primary origin. In one longitudinal section there is a cluster of a few tracheids (fig. 23) which had been cut somewhat obliquely; because of their position near the border of the canal these, too, are thought to be primary xylem. These are the only tracheids in any of the preparations, either longitudinal or transverse, with markings clearly visible; here they are seen as scalariform thickenings on all longitudinal walls.

The carinal canals vary somewhat in shape (figs. 20, 21) but are essentially round in transection with an average diameter of about 350 μ. In comparison with the size of the adjacent pith cells and those of the secondary xylem the canals are larger than in any specimen of calamite I have yet encountered.



Figs 19–23. *Arthroxylon Williamsonii*

Fig. 19. Diagram of reconstruction of transverse section of stem (NR. #4). Figs. 20 and 21. Details of two of carinal canals with pith and radiating secondary elements (NR. #5). Fig. 22. Longitudinal section of portion of pith bordering canal—canal at right (NR. #10). Fig. 23. Cluster of tracheids thought to be primary in origin (NR. #7).

The Secondary Tissues.—In this stem there appears to have been a continuous layer of stelar cambium initiating the secondary tissues, as they form a complete cylinder at the inner margin (figs. 19, 20, 21). Furthermore, the cells are so nearly the same size that under low magnification (32-mm. objective) the transection of the secondary system gives the impression of being a uniform circular band

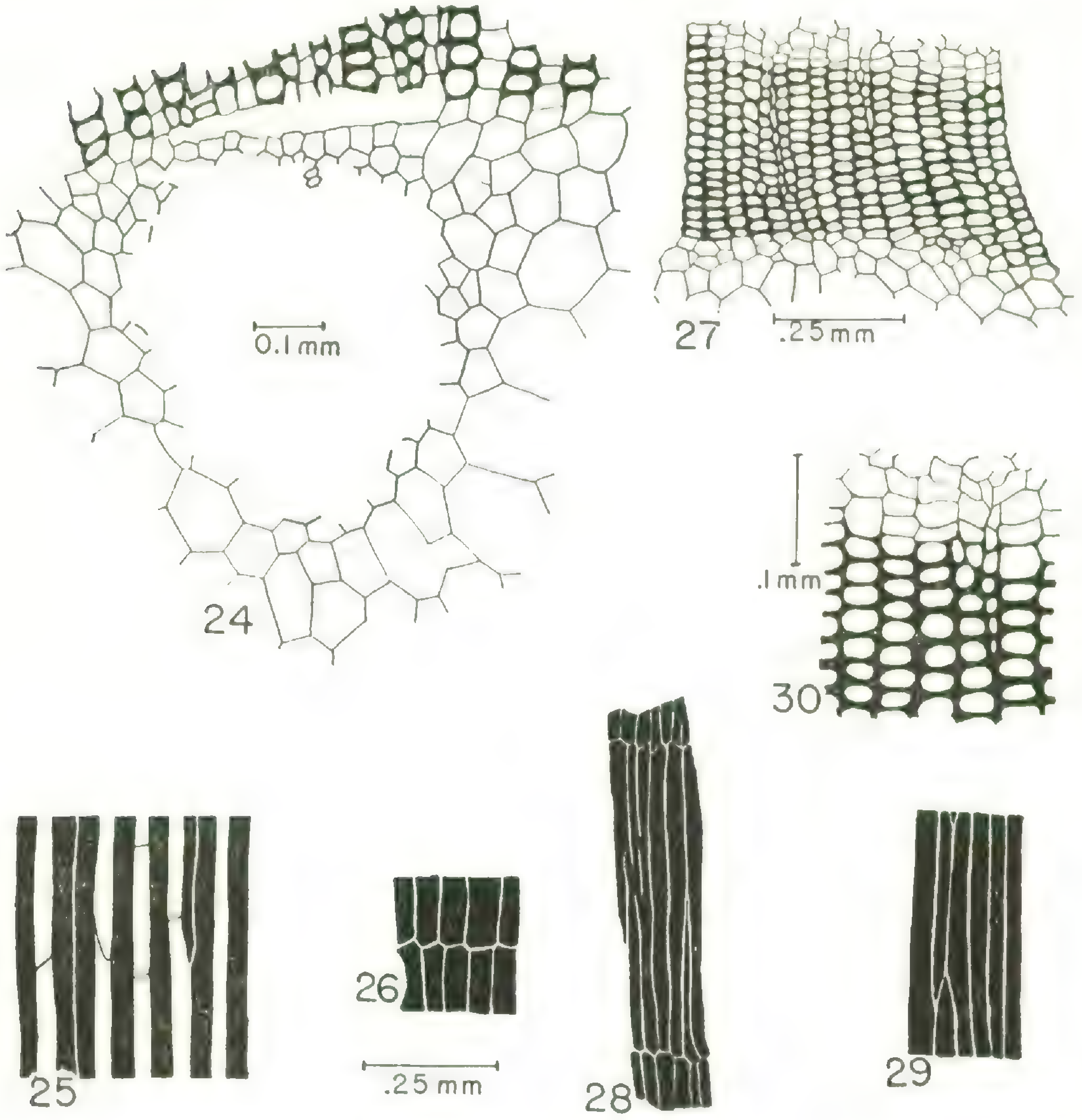
of simple construction with a crenulated outer margin. Yet, when examined under high magnification these tissues resolve into a more complicated pattern. The band of secondary tissues consists of 18–24 layers of cells, the number depending somewhat on the degree of preservation, organized in alternating groups of conducting elements and thick-walled fibrous elements (fig. 19).

Each group of conducting tissue is composed of 14–16 rows of secondary elements radiating centrifugally from the carinal canal; approximately one-third of these are uniseriate rows of thin-walled parenchyma cells which alternate with one to three or even four rows of thick-walled tracheids (figs. 20, 21, 24). In transection the two types of cells, that is, those of the tracheids and parenchyma, are not so different in size or shape, both being squarish with average dimensions of about $25 \times 25\ \mu$, but are to be discriminated chiefly by the difference in the thickness of their walls. However, in tangential section the parenchyma, or "rays" as termed by Williamson, stand out not only because the walls are thinner but also because they are shorter. The available sections scarcely exceed a millimeter in length but in all the end walls were to be found in the parenchyma cells, and there were some instances, as in fig. 25, where both extremities of a cell were found in one field. Occasional end walls of tracheids were encountered, as shown in figs. 25 and 26, but tracheid length was not determined as it was greater than that of the sectioned material.

As the secondary elements were being formed there occurred at intervals anticlinal divisions which increased the number of rows to 28–30 at the outer limit of the woody cylinder. Usually the anticlinal divisions were confined to tracheid initials (figs. 20, 21).

Alternating with the conducting tissue (in transection) are bands of fibrous cells of secondary origin arranged in 18–20 radial rows (figs. 19, 27). There are about as many cells in a row as are found in a row of the conducting region, but the radial diameter of the individual cells is less than that of the tracheids, hence the rows are shorter with consequent decrease in the width of this band of tissue as compared with that of the conducting tissue. It is this difference in width of the two types of tissue that is largely responsible for the fluted exterior of the woody cylinder.

Except for the slight difference in shape of the cells composing it this fibrous tissue bears a striking resemblance, in transection, to the conducting tissue; the cells have thick walls, have an average radial diameter of about $22\ \mu$, and a tangential diameter of $37\ \mu$, and were laid down with the same regularity. Yet, as in the former specimen of *A. Williamsonii* and in *A. oldhamium,* closer observation reveals two differences: (1) there is an absence of the thin-walled uniseriate parenchymatous rows; and (2) there had been fewer anticlinal divisions to increase the number of rows, so that this band of tissue remains essentially the same width from its origin at the pith to the peripheral region of the secondary activity (fig. 27). These differences which are noted in transection are verified by longisection.



Figs. 24–30. *Arthroxylon Williamsonii*

Fig. 24. Detail of cells about the carinal canal (NR. No. 5). Fig. 25. Longitudinal tangential section through the fascicular area (NR. No. 6). Fig. 26. Longitudinal radial section through the fascicular area (NR. No. 11). Fig. 27. Transverse section through the interfascicular area (NR. No. 5). Fig. 28. Longitudinal radial section through fibers (NR. No. 6). Fig. 29. Longitudinal tangential section of fibers (NR. No. 9). Fig. 30. Detail of portion of transection of interfascicular area showing cambium (NR. No. 5).

Figures 28 and 29 are longitudinal (radial and tangential) views of these cells; they are vertically elongated, their length being many times their width, with end walls acutely oblique in tangential view. Their walls all appear to be of uniform thickness with no discernible markings. This tissue, therefore, manifests the same homogeneity of its elements and their organization as was found in the comparable area of the two specimens of *Arthroxylon* from the British Coal Measures.

The meager amount of cambium and phloem preserved, of which fig. 30 shows one of the rare instances, would not be worth recording were it not for the fact that it demonstrates the limit of the activity of the stelar cambium.

Some General Considerations and Key.—

In his account of the types of calamitean stems with structure preserved Scott (1920) wrote of *Arthroxylon (Arthrodendron)*: "The *Arthrodendron* type of stem is a rare one. The wood, in the specimens known, is of no great thickness, and the primary bundles are widely separated by primary medullary rays. The chief peculiarity is in the structure of the rays, which are formed, for the most part, of vertically elongated prosenchymatous cells, thus differing widely from the usual parenchymatous structure of these organs." The calamitean stem from an American coal field, described above, shares these generic characters with specimens of *Arthroxylon Williamsonii* and *A. oldhamium* from the British Coal-Measures.

Because of the disparity of geographic origin it seemed possible that the specimen from Indiana would fall into a third species. However, the size and proportion of tissues and the dimension and organization of cells of the material at hand are so markedly like the type of *A. Williamsonii* that the two key down to the same species.

As for *Arthroxylon* being a "rare type"—one can not help wondering whether a reinvestigation of some of the calamitean stems that have been otherwise labeled might not reveal them to be *Arthroxylon.* In transection (many descriptions have been made from transection only) the bands of fibrous parenchyma cells are almost indistinguishable from conducting tissue unless, as in the specimen of *A. oldhamium*, there had been a selective infiltration of mineral which sharply demonstrated a difference of structure of the cells and differentiated and delimited the two tissues. It seems probable, therefore, that in some cases the fibrous tissue in question has been interpreted as interfascicular xylem.

The question might well arise as to why in the present study no use has been made of the character of the wood stressed by Williamson and Scott (1894). According to them, the wood of *Arthroxylon (Calamopitus)* was "characterized by the predominance of reticulated elements in its wood." However, it is my opinion that one might easily overemphasize this character. These specimens do show, as was noted by Williamson and Scott, scalariform pitting of the primary wood (fig. 23), scalariform to reticulated pitting in the tracheids of the nodal region (fig. 9), and reticulated pitting in the secondary wood (figs. 8, 16). Yet the type of reticulation (pit) may well depend on the differential amount of erosion of the border prior to preservation. Therefore, until more is known of the type of reticulation, that is, of the pit types in calamitean secondary wood, it has been thought best not to stress this feature in the present key and diagnosis.

KEY TO GENERA OF CALAMITE STEMS WITH STRUCTURE PRESERVED, AND TO SPECIES OF *ARTHROXYLON**

1. Secondary interfascicular area composed of parenchyma and tracheids . . *Arthropitys*
1. Secondary interfascicular area composed of parenchyma only.
   2. Interfascicular parenchyma composed of alternating radial bands of thick- and thin-walled cells.......... *Calamodendron*
   2. Interfascicular parenchyma composed of essentially similar cells....... *Arthroxylon*
      a. Interfascicular area of 16–18 rows; radial and tangential diameter of elements 26 × 34 μ.......... *A. Williamsonii*
      a. Interfascicular area of 30–35 rows; radial and tangential diameter of elements 42 × 65 μ.......... *A. oldhamium*

* Based on transection of the internodal region.

Arthroxylon Reed, nom. nov.[4]

Calamopitus Williamson, Mem. Manchester Lit. and Phil. Soc. III, 4:174, figs. 1–17. 1871. (Without type; no species indicated or described).

Calamopitys Seward, Fossil Plants 1:301. 1898. (Without species). Not *Calamopitys* Unger, Denkschr. K. Akad. d. Wiss. Wien. 1:159. 1856.

Arthrodendron Scott, in Seward, Fossil Plants 1:301. 1898. (As subgenus; without type; no species indicated or described). Not *Arthrodendron* Ulrich, Harriman Alaska Series (Smithson. Inst.) 4:138, pl. XIV, figs. 1–3. 1910.

Calamitean stem with internodal region of stele organized in alternating bands (as viewed in transection) of conducting tissue and fibrous parenchyma. Bands of parenchyma as wide or wider than the bands of conducting tissue, composed of fusiform cells with walls as thick as those of the tracheids.

Arthroxylon Williamsonii Reed, sp. nov.

Stems with about 70 large carinal canals (diameter up to 360 μ). Secondary conducting tissue composed of 14–17 rows of tracheids with interspersed rows of parenchyma radiating centrifugally from the carinal canal; the number of rows gradually increased by anticlinal divisions of tracheid initials. Both tracheids and parenchyma roughly squarish in transection with an average dimension of about 22 μ. Bands of fusiform parenchyma cells organized in 18–20 radiating rows, cells with an average radial diameter of 26 μ and tangential diameter of 34 μ.

Horizon: British Coal-Measures; American Upper Carboniferous.

Material: Twelve thin sections (Williamson Collection 35–46) in Geology Department of the British Museum of Natural History; 12 sections (NR 1–12) in the Museum of the Illinois State Geological Survey, Urbana, Illinois.

Type: Williamson Collection No. 35.

Arthroxylon oldhamium Reed, sp. nov.

Secondary conducting tissue composed of 8–10 rows of tracheids with interspersed rows of parenchyma. Very few anticlinal divisions, with the result that the bands of tissue remain virtually the same width from the inner limit at the carinal canal to the peripheral region. Tracheids and parenchyma cells roughly squarish in transection with average dimensions of 44 μ. Bands of fusiform

[4]The generic name is derived from Αρθρον—articulated, and Ζυλον—wood.

parenchyma organized in 30–36 radial rows; cells with average radial diameter of 42 μ and tangential diameter of 65 μ.

Locality and horizon: Sandstone-Quarry near Oldham, British Coal-Measures.

Material: Nine sections (Williamson Collection Nos. 52–60) in the British Museum of Natural History, London.

Type: Williamson Collection No. 52.

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SOME AMERICAN PETRIFIED CALAMITEAN STEMS

HENRY N. ANDREWS*

Descriptions of structurally preserved stems referable to the Calamitaceae (as treated by Hirmer, 1927) are notably few in the American literature. A fragmentary calamitean stem was reported by Reed in 1926, and the same author later (1938) described a young stem under the name *Calamites multifolia*. Several other authors have recorded the occurrence of petrified calamitean stems in American coal balls (see Andrews, 1951), but no comprehensive or critical accounts have been given previously.

Up until a few years ago the numerous coal balls which had been cut in my laboratory revealed almost no fossils of this group. This was rather puzzling in view of the fact that pith casts and foliage referable to the Calamitaceae are not rare in the American coal fields. Apparently, our earlier collections had been made from spots where calamitean stems did not chance to have been deposited, for during the past four years we have accumulated stems and roots in some abundance.

The specimens described here came from several localities in Illinois, Iowa, Indiana, and Kansas, and represent the three genera *Arthropitys*, *Arthroxylon* and *Calamodendron*. Certain of the species are closely comparable with European ones while others show quite distinctive characters. Several specimens have come from the Calhoun horizon in the upper part of the McLeansboro group in southern Illinois; some are from the Petersburg No. 5 coal north of Booneville, Indiana; several coal balls containing well-preserved stems and roots have been turned over to me by Dr. A. H. Blickle who collected them near Oskaloosa, Iowa. However, by far the most prolific source has been the vast coal-ball supply in the Fleming coal which is mined near West Mineral, Kansas. At this last locality it is evident that the calamites composed a significant element of the Carboniferous vegetation. More precise data concerning the horizons at which these plants were found will be given under the species descriptions, and for additional information the following references may be consulted: Abernathy, 1946; Andrews, 1951; Schopf, 1941; Andrews and Mamay (1952).

Although the generic name *Calamites* was originally assigned to pith casts where the cellular structure was unknown it has been generally applied in a rather loose manner to both stems and plants as a whole. In the following pages I will use the term "calamitean" to refer to stem remains of plants referable to the Calamitaceae as defined by Hirmer (1927, p. 381).

In many cases it is rather easy to recognize calamitean stems in a freshly cut coal ball or where they are exposed on a weathered surface prior to any treatment. The lack of much pith tissue, presence of protoxylary canals, and characteristic banded appearance of the secondary wood are distinctive characters. It is quite another matter to identify the fossils specifically, and as Miss Reed has pointed out

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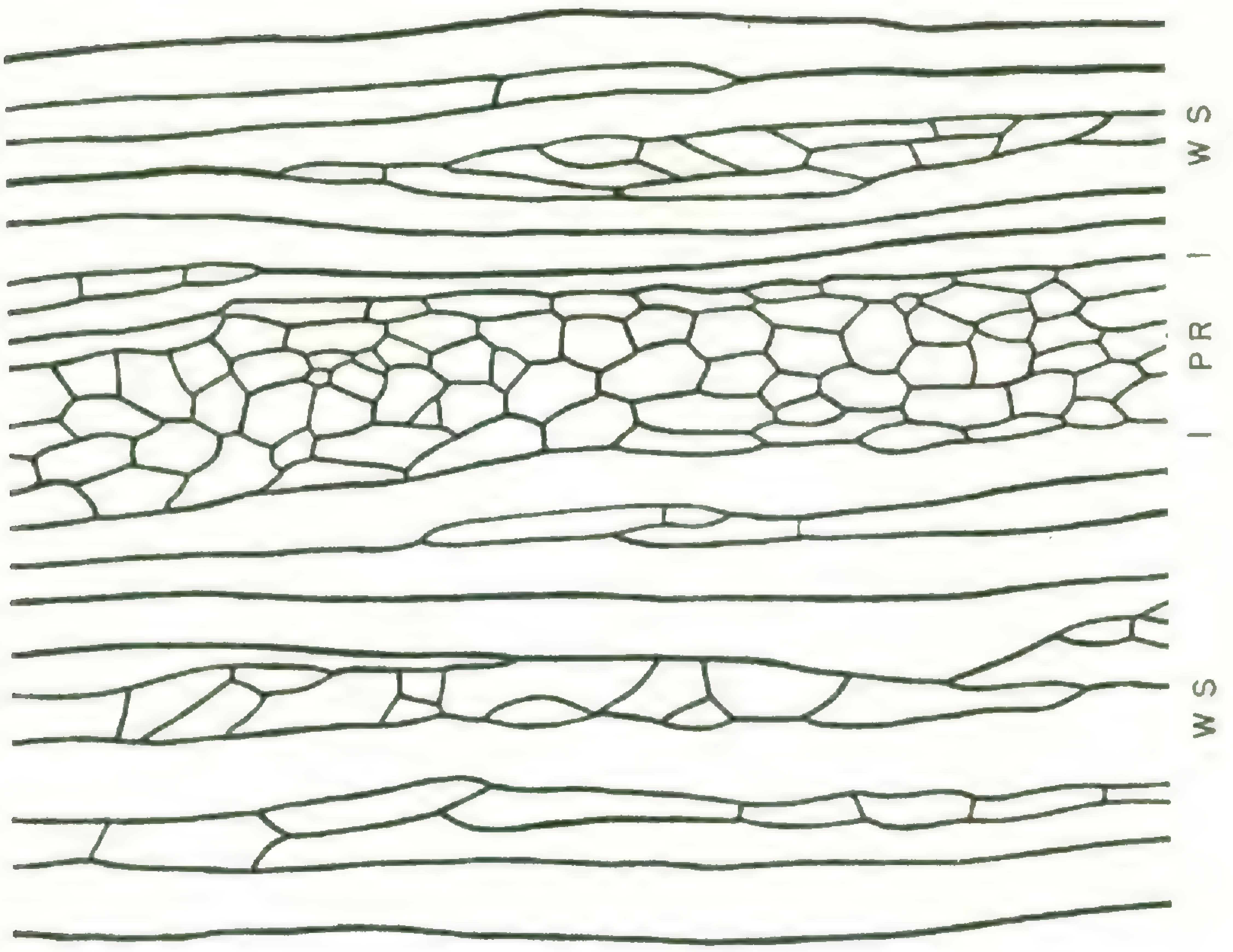
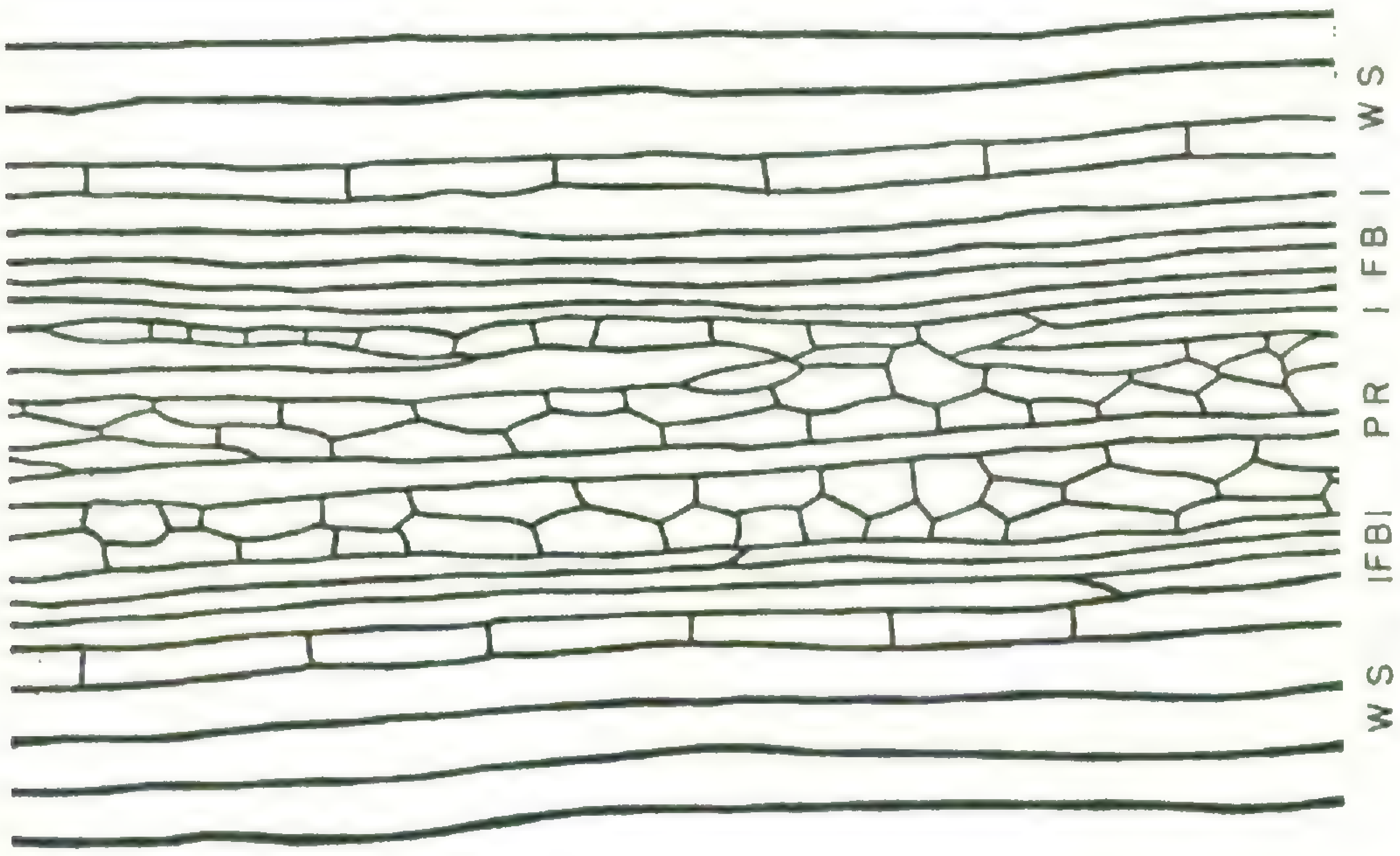
* John Simon Guggenheim Memorial Foundation Fellow at Harvard University, 1951.

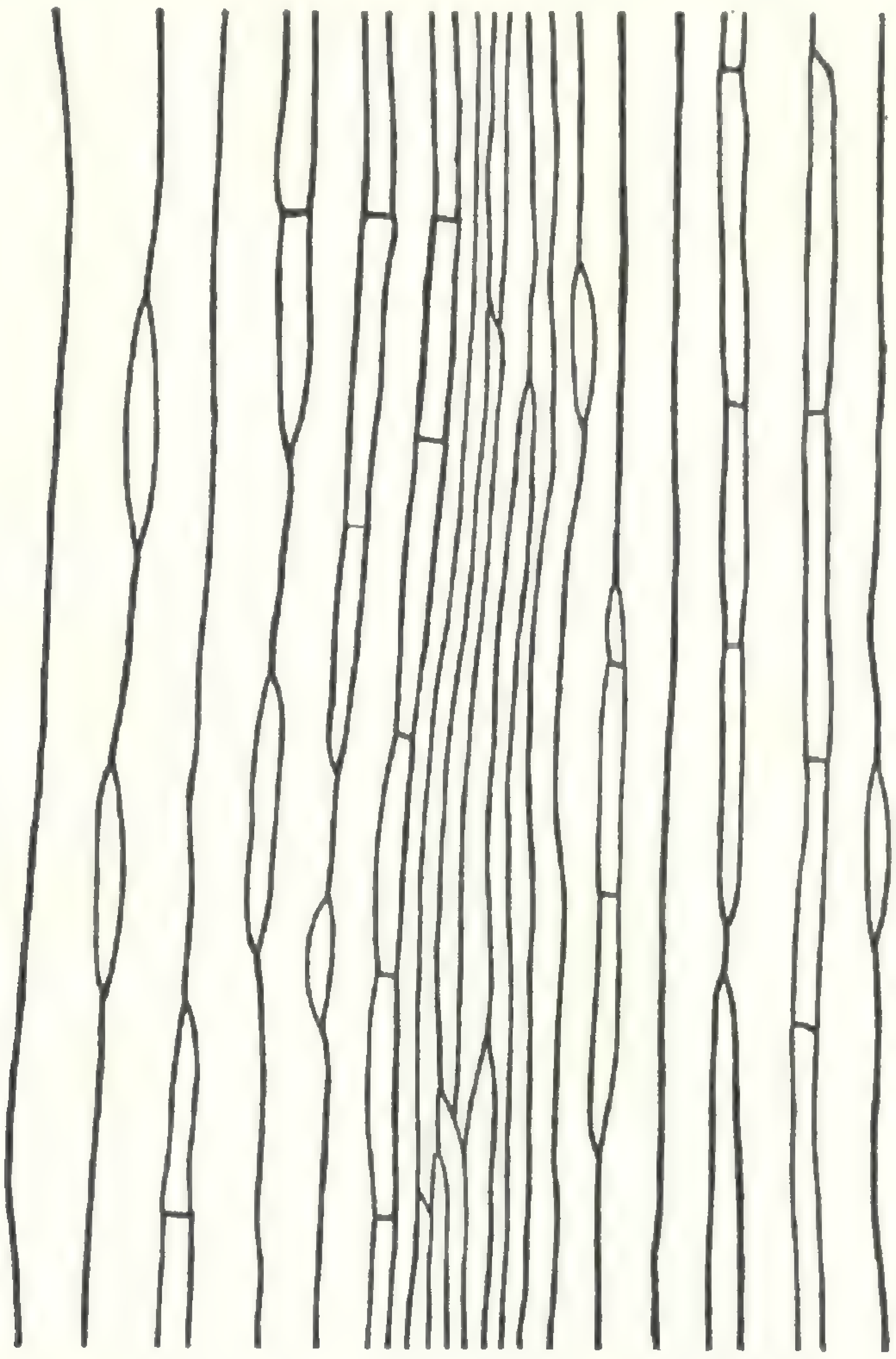


Text-fig. 2. *Arthropitys kansana*



Text-fig. 1. *Calamodendron americanum*

Text-figs. 1–3. Tangential sections of *Calamodendron, Arthropitys,* and *Arthroxylon* respectively, showing the comparative anatomy of the wood; all are camera-lucida drawings × 35: WS, wood sector; FB, fiber band; PR, primary ray.



Text-fig. 3. *Arthroxylon Williamsonii.*

in the preceding contribution, tangential sections are necessary for positive generic identification. In order to discuss this problem I shall devote more space than is ordinarily necessary to brief reviews of the history and taxonomic status of the genera concerned. Much of the pertinent literature is not readily available, and since it is evident that our work to date is only introductory to the American fossils of this group it is hoped that the supplementary information presented here may be of aid in future studies. A considerable number of genera of articulate cones are now known from American coal balls, some of them of excellent preservation and distinctive organization, yet much remains to be accomplished in classifying the stem remains and correlating them with the cones.

The petrified calamitean stems are known chiefly from the works of Williamson, Scott, Renault, and the more recent contribution by Knoell. Williamson and Scott, in their several papers on these fossils, have given us an excellent general understanding of the curious stem anatomy, but taxonomic considerations appear to have been of less concern to these English workers. Little attention was given to specific entities of *Calamites* (stems now assigned to *Arthropitys*), and in the unique *Arthroxylon*, a fossil described and illustrated in excellent fashion by

Williamson as long ago as 1871, no specific name has been assigned prior to Miss Reed's present account. Renault, on the other hand, has recorded a considerable number of species of *Arthropitys* and several of *Calamodendron*. While certain of these are based on specimens that are insufficient in size or preservation to allow the establishment of a significant binomial, they serve to convey a knowledge of character variation in the group. Knoell's contribution (1935) adds to our knowledge of the group but in the present writer's opinion depends too heavily on transverse sections. The reason for this criticism will be apparent in the following pages.

The petrified calamitean stem remains are segregated into three genera: *Arthropitys, Arthroxylon* and *Calamodendron*. Before considering each in detail it may be useful to record the distinctive generic characters.

Arthropitys Goeppert, 1864

The wood sectors[1] are separated by primary rays which vary from one to several cells wide. In many species the primary rays are broad conspicuous bands, and they may extend undiminished to the outer periphery of the xylem or taper abruptly. In the latter instance the outer portion of the secondary wood consists of a more or less uniform mixture of tracheids and small rays. The ray cells in all cases are more or less brick-shaped (text-fig. 2).

Calamodendron Brongniart, 1849

The wood sectors are separated from the primary rays on either side by fibrous bands, the radial sequence thus being: wood sector, fiber band, primary ray, fiber band, wood sector, etc. The fiber bands flanking the wood sector may equal the latter in (tangential) thickness or be considerably less (text-fig. 1).

Arthroxylon Reed, 1952

The wood sector appears essentially similar to that of the two genera cited above. The primary rays, however, consist of vertically elongated cells several times as long as broad and present a striking contrast with *Arthropitys* or *Calamodendron* or in fact with the "rays" of any other stem exhibiting secondary wood (text-fig. 3).

In so far as these three genera are known the significant features lie in the secondary xylem. Several authors have described specimens of small twigs in which little or no secondary growth is present, and in some cases specific names have been applied to such remains. While future studies may reveal ways of identifying more precisely such remains, a comparison with any of the above-cited genera usually appears to be arbitrary. One must have a way to handle such specimens, and Reed's (1938) solution of assigning them to *Calamites* seems satisfactory. There is no reason to doubt that the three genera, *Arthroxylon, Calamo-*

[1] The secondary xylem of most calamitean stems is composed of two distinct tissue systems: the *wood sectors* which radiate from the protoxylary canals and consist of tracheids and small rays; and alternating *primary rays* which are in direct contact with the pith and are parenchymatous in nature. The term *secondary ray* is used here to refer to the (usually uniseriate) rays which occur interspersed among the tracheids in the *wood sector*.

dendron, and *Arthropitys,* so distinct in the organization of their secondary wood, are all responsible for the common pith casts assigned to *Calamites.* The latter is thus a more "inclusive" genus and perhaps suitable for small petrified stems.

In only a few instances have stems been reported in which the cortical tissues are preserved. One such specimen described as a "Calamite stem" by Seward (1898, fig. 78) indicates that a considerable abundance of cork tissue was present in the larger branches.

A point that is deserving of special note here is the problem of distinguishing the three genera in transverse section. It may be that with especially well-preserved specimens and much experience on the part of the investigator this is possible, but the rather close similarity of the several cell types involved renders it otherwise difficult. In *Calamodendron,* with its fibrous bands between the wood sector and primary ray, the transverse section may reveal the specimen's generic affinity but with the other two the problem is more acute. In the case of the *Arthroxylon* reported below I assumed from the transverse section that it was a species of *Arthropitys,* and it was only when the tangential section was studied that the distinction became evident.

Arthropitys Goeppert

There have been some eighteen or more species and varieties assigned to this genus although several of them are based on fragmentary and incomplete material. Most of the descriptions are to be found in the contributions of Renault, Goeppert, and Knoell, cited below.

A considerable degree of variation is present in the organization of the primary ray. It may retain a considerable breadth throughout the secondary xylem; it may taper off quite abruptly; or be lacking from the start, although in a single specimen the organization is generally quite constant. When the primary ray tapers rapidly the anatomy presented by a tangential section must be carefully correlated with the transverse view. For example, figs. 6 and 7 illustrate the difference that may be encountered in a single specimen. Care must also attend the use of the transverse section with reference to its proximity to the node.

Other characters have been used such as the size of the stem, extent of secondary growth, length of internode, nature of the tracheidal pitting, and the size of the protoxylary canals. Of these characters, the first two are obviously a reflection of ontogenetic development and require no further comment. The length of the internode may be significant if the specimens are long and abundant and thus subject to statistical analysis, but it seems of doubtful value with a small isolated specimen. With reference to the pitting, both scalariform and the round, crowded bordered pits are found in the genus. In any individual specimen one type is usually predominant although transitions are not uncommon. The size of the protoxylary canals varies considerably, and this may be of use as a supplementary character. Renault has reported one specimen *(A. gigas)* in which they are

lacking. In this connection I would like to note that certain of the specimens of *Arthropitys* that I have examined appear to display tracheids internal to the protoxylary canal. A more detailed discussion of this will be found under the description of *Arthropitys* sp. A.

This account is by no means intended as a monographic treatment of the genus. It seems useful, however, to cite briefly below the supposedly distinct features of certain species as a matter of recording structural variation in the genus and for the purpose of comparison with the American fossils.

Arthropitys bistriata (Cotta) Goeppert, 1864

As figured by Renault, 1895 (see especially pl. 4, fig. 3; pl. 5, figs. 8, 9), the secondary wood is composed of uniform wood sectors and primary rays, the latter being 6–7 cells wide (nearly as broad as the wood) and extending vertically from one node to the next. Small rays are present in the wood sectors. The pitting of the tracheids appears, in Renault's figures, to be predominantly scalariform with a tendency toward reticulate-bordered arrangement. This species is based on Cotta's *Calamitea bistriata* described in 'Die Dendrolithen', and I believe should be accepted as the type species. Goeppert's figures do not display all of the distinctive characters as well as might be desired. For example, his fig. 1 on pl. 33, a transverse view of a portion of the stele, does not show the protoxylary canals. Renault's description (1895) is very thoroughly illustrated. Origin: Permian, Chemnitz, Germany.

Arthropitys communis (Binney) Hirmer & Knoell (in Knoell, 1935)

This species was originally described by Binney (1868) as *Calamodendron commune*. It is discussed by Williamson and Scott, 1895, and in Williamson's earlier contributions. While presenting splendid anatomical studies Williamson and Scott were not concerned with the assignment of specific names. The most recent treatment is that of Hirmer and Knoell (in Knoell, 1935) where the plant is formally assigned to *Arthropitys*. This is a species which attained considerable size; it possesses scalariform pitted tracheids and large primary rays which usually taper rather abruptly.

Arthropitys ezonata Goeppert, 1864

This species is based on a rather small fragment. The primary rays appear narrow, little larger than the rays in the wood sector; the pitting is scalariform. Origin: Permian; Chemnitz, Germany.

Arthropitys gallica Renault, 1896

This is represented by a large stem reported to be 24 cm. in diameter (apparently this refers to wood only). Numerous resin cells are present in the peripheral pith zone, and the tracheids display scalariform pitting. The primary rays are initially broad but do not remain so throughout the wood as in *A. bistriata*. It is reported to differ from *A. approximata* (see below) by its over-all size and length of internodes, characters which seem to be of doubtful significance. Origin: uppermost Carboniferous; Montrambert, near Saint Etienne, France.

ARTHROPITYS APPROXIMATA (Schlotheim) Renault, 1896

According to Renault, "Cette espèce se distingue facilement de l'*Arthropitus bistriata* par sa taille plus petite, par ses entre-noeuds qui sont plus courts, par ses verticilles ramifères qui sont plus fréquents" (1896, p. 310). It is my feeling that these characters, while they may distinguish a *specimen,* actually are of little specific value. Origin: Upper Carboniferous; Saint Etienne, Commentry, Autun, in France.

ARTHROPITYS LINEATA Renault, 1876

Large primary rays are initiated in this species but almost immediately disappear, so that the secondary xylem for the most part consists of tracheids rather regularly interspersed with small rays. The tracheids are scalariform.

ARTHROPITYS MEDULLATA Renault, 1896

This species is apparently very similar to *A. lineata* in the general organization of the secondary wood. It is reported to have a small pith (cavity) and relatively abundant wood. Origin: Upper Carboniferous; Autun, France.

ARTHROPITYS GIGAS (Brongniart) Renault, 1896

This is a large species described as attaining a diameter of 50 cm. The tracheids bear numerous rows of round pits, and protoxylem canals are reported to be lacking. Origin: Permian; Autun, France; the "grès rouge inférieur de Saarbruck; and the grès cuivreux de Nidji-Troisk, district de Bjelebey, de Piskork, Orenbourg, Russia."

ARTHROPITYS ROCHEI Renault, 1896

This is also represented by large specimens. It is distinguished from *A. gigas* by the presence of protoxylary canals as well as more numerous and larger secondary rays in the wood sectors. The tracheids display numerous bordered pits. Origin: Upper Carboniferous and Permian; Champ des Borgis, France.

ARTHROPITYS BISTRIATOIDES Hirmer & Knoell (in Knoell, 1935).

The secondary wood is present but not strongly developed; the primary rays and wood sectors appear to maintain equal tangential dimensions. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

ARTHROPITYS HIRMERI Knoell, 1935

The secondary wood is strongly developed and homogeneous, no large primary rays being present. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

ARTHROPITYS JONGMANSI Hirmer (in Knoell, 1935)

Very little secondary growth is present; the protoxylary canals are very large and the primary bundles numerous; abundant thick-walled parenchyma cells form conspicuous arcs on the inner side of the canals. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

Arthropitys herbaceae Hirmer & Knoell (in Knoell, 1935)

The central (pith) canal is large, and almost no secondary wood is present. There are certainly no distinctive characters here, and the authors admit that it may be only a young condition of some other species.

In spite of the difficulty of defining clear-cut species of *Arthropitys* it is evident that there is considerable variation. Aside from the difference in pitting the most striking feature is the variation in wood sector-primary ray relationship, and it seems possible to the present writer that this may serve as a reasonable basis for further generic segregation.

Arthropitys communis (Binney) Hirmer & Knoell, var. **septata** Andrews, var. nov.

The following description is based on specimens No. 722 and 804 found in coal balls from the Calhoun horizon near Berryville, Illinois.

The most complete specimen (figs. 1, 2) consists of a stem fragment about 18 cm. long and a maximum diameter of the secondary wood of nearly 7 cm. The phloem and cortical tissues are not preserved. If, however, abundant periderm was developed, as described by Seward (1898, figs. 78, 79) for certain English specimens of *Arthropitys*, this one from Berryville represents a trunk of 6–8 inches in diameter.

The stem presents a striking appearance by virtue of seemingly large, more or less oblong "canals" in the periphery of the pith. These are well shown in fig. 1. Although the "canals" probably represent decay areas and consequently are of no taxonomic significance, their regular arrangement suggests some sort of cellular differentiation. Another specimen has been observed which shows a tendency of the pith cells to disintegrate at rather regular intervals around the periphery. This decay, if carried further, would produce the effect shown in fig. 1.

Certain of the pith cells in the peripheral region are larger than the others and display dark contents which suggest a secretory nature. However, in all, it is not easy to distinguish these apparent secretory products from iron sulphide. Renault has reported resinous cells in the pith of *A. gallica.*

Outside of the pith the preserved part of the stem consists of a strongly developed zone of xylem which attains a (radial) width of about 15 mm. This consists of scalariform tracheids and parenchymatous rays. Before considering the secondary tissues in detail we may note first the protoxylary canals which are very small and at many points appear to be lacking. Slight differences in the quality of preservation make it difficult to appraise these at all points but in places where the preservation is excellent no canal can be observed and at others only small ones are to be noted (fig. 10). Renault (1896) reported protoxylary canals lacking in *A. gigas.*

Figure 2, a representative sector of the secondary xylem, shows radially elongate wedges of tracheids (wood sectors) separated by broad parenchymatous primary rays. Going radially from pith to periphery of the wood it will be noted that the

rays gradually decrease in their tangential dimensions or rather lose their distinctive appearance by the admixture of rows of tracheids.

The tracheids are uniformly scalariform (fig. 8), and their morphology presents a point of some interest. When first studying tangential sections taken only a few cells from the protoxylary canal I observed what appeared to be a considerable admixture of rays, a rather surprising point since such rays were not evident in the transverse view. Further observation with both radial and tangential sections revealed that the tracheids are profusely septate (fig. 5) near the inner limits of the secondary wood, the septations being for the most part horizontal walls. The tracheids average about 44 μ in diameter, and the length of the inner secondary tracheids may likewise be no more than 44 μ. That is an extreme case but cells 100 μ long are not uncommon although lengths are very variable. At a distance of 2 mm. farther out, the tracheids are many times longer than wide; in fact, it is nearly impossible to follow cells through their entire length due to the interference of rays, but the septations are still evident. Scott (1920, p. 25) mentions the occurrence of transverse walls in the tracheids but indicated that they are not frequent; his discussion of calamitean anatomy is rather general but he is presumably referring to *Arthropitys communis*. In this specimen from Illinois the septations are very abundant and it was not until several mm. of secondary wood were formed that the tracheids assumed great length and predominantly tapered ends.

The primary rays (figs. 1 and 10) are initiated as broad parenchymatous bands of .5 mm. or more in width and extend vertically from one node to the next. In passing out radially through the wood two changes are notable; the tangential dimensions of the primary rays gradually decrease until, at a distance of 6–7 mm. from the pith, they are no longer readily distinguishable. This statement is of course subject to a certain amount of variation; the second change is in the decrease in size of the cells composing the rays.

As might be surmised, the tangential sections present corresponding differences depending on their position from the pith. Figures 6 and 7, shown at the same magnification, display the tangential aspect at points .5 and 11 mm. respectively from the pith.

The more striking features of these sections may be noted briefly:

Figure 6.—The primary ray cells, although very variable in size, range up to 120 μ in width (tangential). The structure of the wood sector is not easy to interpret due to the presence of a considerable number of septate tracheids, but it appears that secondary rays have already been initiated.

Figure 7.—The ray cells are generally smaller, not often exceeding 70 μ in tangential dimensions. The tracheids are greatly elongated and are interspersed with abundant secondary rays which are 1- to 3-seriate and of very variable height. When observed in radial view the ray cells appear (fig. 9) quite uniform in size, averaging about 44 μ wide and 108 μ high.

A comparison of this Illinois *Arthropitys* with the better-known species described by Renault and by Knoell seems to indicate that the closest relationship lies with *A. communis*. The comparison is close although there are certain differences which seem to justify at least varietal distinction. These differences are principally: (1) the small size of the protoxylary canals; (2) the abundant septation of the tracheids in the earlier formed secondary xylem; (3) the lack of pronounced tangential elongation of certain of the cells of the primary rays (cf. Knoell, 1935, pl. 2, fig. 6A).

Diagnosis:

Primary rays diminishing in tangential dimensions rather rapidly; protoxylary canals small and sometimes lacking; inner tracheids profusely septate; secretory cells present in pith.

Horizon and age: Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Locality: Brian farm, near Berryville, Illinois.

Type specimen: Coal ball No. 722, Henry Shaw School of Botany, Washington University, St. Louis.

A Small Calamitean Stem from Berryville, Illinois.—

A few very young calamitean stem specimens may be recorded briefly although their development is not sufficiently advanced to allow generic designation.

Two small stems, one of which is shown in fig. 4, have been found which measure about 1.3 mm. in diameter. They consist of only a few layers of pith cells, about a dozen protoxylary canals, and a broad cortex. A few tracheids may be noted around the outer periphery of each canal, resembling in this early stage the structure in the modern *Equisetum*. The phloem cannot be observed, a break between the xylem and inner cortex apparently representing the cavity left by the decay of that tissue. Numerous cells in the inner part of the cortex are distinguished by having either dark, thick walls or a dark (resinous?) substance in the periphery of the cell lumen.

In the same coal ball (No. 756) which contained these minute stems a somewhat larger stem appears with secondary growth evident. The same dark substance may be noted in some of the inner cortical cells as indicated above, and there seems to be little doubt that this is a somewhat older stage. Although there is not a great deal of secondary xylem developed in this specimen (fig. 13), it seems very possible that it belongs to *Arthropitys* and by virtue of the similarity of the cortex one may infer that the smaller stems (fig. 4) do likewise.

Calamitean Stems from Kansas.—

Numerous calamitean stem specimens have been obtained from the strip pit of the Pittsburg and Midland Coal Mining Corporation located about four miles south of the town of West Mineral, Kansas. This horizon is the Fleming coal which occurs in the upper part of the Cherokee shale and is approximately of mid-Pennsylvanian age. Coal balls are found here in an unparalleled abundance (see

Andrews and Mamay, 1952), hundreds of tons of them being used for road-building material. A considerable portion of them are heavily pyritized although specimens of excellent quality are not rare.

By comparison with any other American coal ball locality with which I am familiar, or with any reported in the literature, the calamitean stems are notably abundant. We have encountered some scores of specimens, although many of the strongly pyritized ones have been discarded in the field; from the abundant specimens several distinct species have been recognized.

ARTHROPITYS **kansana** Andrews, sp. nov.

This description is based on specimen Nos. 755 and 786. No. 755, which is designated as the type, is a nearly complete transverse section of a stem (fig. 14) in which the xylem attains a thickness of 14 mm. No. 786 is a fragmentary sector of a larger stem in which the xylem attains a thickness of about 23 mm. and probably represents a stem of 8–10 inches in diameter. Both specimens are partially pyritized, although No. 786 is notable in that certain portions of the wood are quite lacking pyrite and are exceptionally well preserved. There is an appreciable thickness of pith tissue present, and the protoxylary canals are rather large, averaging about 200 μ in diameter.

The most distinctive feature of the wood lies in the uniform width of primary rays and wood sectors throughout the extent of the xylem (fig. 14). There is to be sure some variation in organization of the primary rays. They tend to lose their identity by the admixture of tracheids in their outer course but for the most part they continue more or less undivided, and the contrast with the *communis* type (fig. 2) is rather striking. As viewed in tangential section (fig. 11), the primary rays may be noted to extend vertically from one node to the next, and aside from the occasional interruption by a tracheid they are quite uniform in their tangential dimensions. The wood sectors consist of tracheids (fig. 12) interspersed with secondary rays (figs. 11, 17, 26) of very variable dimensions. The latter may be uniseriate and only 2–3 cells high, and at the other extreme rays 3–4 cells wide and many cells tall are present.

This *Arthropitys* from Kansas seems to compare most closely with Renault's species *A. rochei* and *A. porosa*. The tracheid-ray relationship, however, does not seem to be sufficiently close to admit inclusion in either of these species a certainty. Renault's illustrations of *A. rochei* are not adequate to allow accurate comparison. *A. porosa* is based on a small fragment but judging from Renault's (1896) fig. 7, pl. 7, the Kansas fossil differs most notably in the abundance of secondary rays.

Diagnosis:

Stem with strongly developed secondary wood; protoxylary canals relatively large; primary rays narrow but uniform throughout the radial extent of the wood; woody sectors interspersed with numerous secondary rays which vary much in size; radial walls of tracheids with circular to slightly elongate bordered pits.

Horizon and age: Fleming coal, upper part of Cherokee shale, Missouri series; mid Pennsylvanian.

Locality: from strip mine located four miles south of West Mineral, Kansas.

Type specimen: coal ball No. 755, Henry Shaw School of Botany, Washington University, St. Louis.

ARTHROPITYS sp. A

Our Kansas collections include a specimen (No. 805) which is interesting in several respects but because of imperfect preservation I hesitate to assign a specific name to it. It consists of a fragment of a stem the woody cylinder of which must have exceeded 6 inches in diameter, thus representing a stem perhaps a foot or more thick in life. Some concept of its size may be gained from the fact that the wood attains a thickness of 5 cm. Unfortunately, the pith tissue is entirely decayed and the wood is rather badly shattered.

When viewed in transverse section the protoxylary canals (figs. 16, 23, 24) appear to be surrounded by a distinctive band of thick-walled cells which seem to represent an appreciable development of centripetal wood. Series of longitudinal peels were prepared through several of the canals in an attempt to determine the nature of the pitting of these cells. Although they are thick-walled and of great length, quite in contrast to the pith cells, I have been unable to observe any specialized thickening of the wall to confirm the supposition that they represent centripetal wood. The first 3–4 centrifugal cells also lack pitting, evidently through lack of preservation, so that I believe there is no reason to doubt that the inner cells represent centripetal tracheids. Aside from these small cells immediately surrounding the protoxylary canal, the tracheids show predominantly very elongate bordered pits. Occasionally, however, circular bordered pits may be observed.

ARTHROPITYS sp. B

This (No. 753) is another rather large stem the woody cylinder of which must have been about 5 inches in diameter in life. It is quite similar to that of *A. kansana* except that the tracheidal pitting is predominantly scalariform (fig. 21). Certain areas, however, show a tendency toward the reticulate-bordered type (fig. 22). From my own observations and judging from previously described species the nature of the tracheidal pitting in the secondary wood of the calamitean stems is quite constant, being either scalariform or of the reticulate-bordered type.[2] In view of the variation displayed in this specimen, however, I am reluctant to assign it a distinct specific name. It is of interest from the standpoint of variation in characters displayed by these several Kansas specimens, but it seems desirable to await further information before making a binomial committment.

[2] It may be noted, however, that Renault shows a remarkable combination of multiseriate bordered circular to elongate pitting (nearly scalariform) in *Calamodendron intermedium* (Renault, 1898, pl. 2, fig. 3). His figures indicate that a particular cell is clearly of one pattern or the other, which lends a rather striking appearance.

CALAMODENDRON Brongniart

The genus *Calamodendron,* characterized chiefly by the fibrous cells which occupy a position between the wood sector and primary ray, is represented in the author's collection by one specimen from the Mineral, Kansas, locality.

Three species have been described by Renault which may be briefly characterized:

CALAMODENDRON STRIATUM Brongniart (see Renault, 1898, p. 381).

Relatively narrow fibrous bands are found on either side of the woody sector and the primary rays are narrow. Renault's fig. 4, pl. 1, shows the fibrous band as consisting of about 6–8 cells and indicates uniformity throughout the xylem. The tracheids bear elongate pits. Origin: Permian (Rotliegendes); Champ des Borgis and Margenne, France.

CALAMODENDRON CONGENIUM Grand 'Eury (see Renault, 1898, p. 386).

The wood sectors are narrower than the flanking fibrous (prosenchymatous) bands, thus presenting a relationship inverse to that found in *C. striatum.* The tracheids display multiseriate bordered pits. Origin: Upper Carboniferous; Saint Etienne, France.

CALAMODENDRON INTERMEDIUM Renault (1898, p. 371).

The general relationship of the primary rays, fiber bands, and wood sectors is similar to that of *C. congenium.* The tracheids have elongate bordered pits as in *C. striatum* or multiseriate bordered pits as in *C. congenium,* whence the specific name. Origin: Upper Rotliegendes; Autun (Champ de Borgis), France.

CALAMODENDRON **americanum** Andrews, sp. nov.

This species is represented in our collections from Kansas by one specimen (No. 709) 27 cm. long with a woody cylinder 26 mm. in diameter. The pith area, although not preserved, is small, measuring about 3.5 mm. in diameter, and the wood attains a radial thickness of about 11 mm.

In view of the lack of pith, of protoxylary canals, and extra stelar tissues, the description is necessarily based on the secondary xylem (fig. 29). When viewed in tangential section, the primary rays are seen to be flanked on either side by 3–5 fibrous cells, and the ray proper is occasionally interspersed with the fibrous cells. The latter are, for the most part, readily distinguishable from the tracheids, being thicker-walled and averaging about 16 μ in diameter while the tracheids are about twice that size.

The smaller secondary rays may be observed scattered among the wood sectors although the heavy pyritization of that part of the wood renders study difficult. The tracheids are of the multiseriate bordered type.

When compared with the three species described by Renault the fibers (prosenchymatous cells) in our specimen are not nearly as prolific as in *C. congenium* or *C. intermedium.* As far as the wood sector-fiber-primary ray relationship is

concerned it compares much more closely with *C. striatum*. However, the Kansas fossil shows somewhat less fibrous tissue than *C. striatum* and the rays of *C. americanum* appear less regular; that is, they tend to be more frequently interspersed with fibrous cells than is indicated by Renault's fig. 5 (1898). An additional difference is the very elongate, almost scalariform tracheidal pitting reported in *C. striatum*, whereas *C. americanum* has the multiseriate-bordered type, presenting a striking contrast.

Diagnosis:

Pith area small, about 3.5 mm. diameter; primary rays flanked on either side by 3–5 rows of fibrous cells which also occur interspersed in the primary rays; fibrous cells with thicker walls than tracheids and smaller diameter; some small rays present in the wood sectors; tracheids with multiseriate circular bordered pits in radial walls.

Horizon and age: Fleming coal, upper part of the Cherokee shale, Missouri series, mid Pennsylvanian.

Locality: from strip mine located about four miles south of West Mineral Kansas.

Type specimen: No. 709, Henry Shaw School of Botany, Washington University, St. Louis.

Arthroxylon Reed, 1952

The curious taxonomic history of the fossils now included in this genus is given by Miss Reed in the preceding article.

Arthroxylon Williamsonii Reed

The following description is based on several stem specimens collected by Dr. A. H. Blickle at the Argus coal mine two miles north and three miles east of Oskaloosa, Iowa. Associated with them were several other coal balls containing calamitean roots. It seems very likely that these are the roots of this species but organic connection thus far has not been proven. Another specimen of *Arthroxylon* (No. 750), obtained from the West Mineral, Kansas, locality, is probably referable to this species. There is, however, an element of doubt involved and when additional specimens are discovered, it may be necessary to recognize this as a distinct species.

When viewed in transverse section, *Arthroxylon* cannot be distinguished from *Arthropitys*. However, in a tangential section the departure of *Arthroxylon* is very striking, the distinction lying in the vertically elongate nature of the cells composing the primary rays (cf. text-figs. 2, 3). This is a character which distinguishes *Arthroxylon* not only from other articulate genera but from all other vascular plants so far as I am aware.

Figure 15 shows in transverse view a representative portion of a stem. In the specimens the primary rays appear appreciably darker than the wood sectors due apparently to slightly thicker cell walls. Although only about 2.5 mm. of sec-

ondary wood are present the primary rays retain their identity essentially unchanged through that distance.

A distinctive feature of the stem lies in the nature of the inner limits of the xylem. The wood sector and primary rays form a very uniform line (fig. 15), that is, the pith does not extend into the xylem between the wood sectors, and the distinctive cellular organization of the primary "ray" is reflected in this sharp demarcation line between pith and xylem. The protoxylary canals thus assume an even more conspicuous position than is usual in the other two genera, and they are bounded on their lateral and inner walls by a layer about two cells deep of relatively small and thick-walled cells.

The primary "rays" are composed of greatly elongate cells which average about 30 μ in diameter and are in excess of 3 mm. long (fig. 19); thus their length is at least 100 times that of their diameter. It is not possible to measure the length accurately but this approximation will suffice to show the striking contrast with the primary ray of *Arthropitys.*

The wood sector consists of two types of cells, the greatly elongate tracheids, and secondary "ray" cells which are also unique in their organization (fig. 20). The latter are smaller than the tracheids, averaging about 30 μ in diameter, and are as long as .5 mm. The size and organization of these cells vary considerably, however. A ray may consist of a single cell which may be as little as .15 mm. long or as tall as .3 mm., but most of the rays consist of several cells each ranging from .3 to .5 mm. tall, and the ray as a whole may be several mm. tall. When observed in a perfect radial section (fig. 18) they present the storied effect found in certain dicotyledons.

Roots Associated with Arthroxylon Williamsonii.—

The calamitean roots have been dealt with in some detail by Renault (1885) and by Williamson and Scott (1895). These authors have pointed out their distinct characters but we still know very little about the respective identity of the roots of the three stem genera.

Williamson and Scott cite the following characters which in general serve to distinguish the roots from the stems:

1. Centripetal development of the primary xylem.
2. Alternate arrangement of the primary groups of xylem and phloem.
3. Endogenous mode of origin of the organ itself and of its branches.
4. Absence of nodes.

To which the following may be added:

5. Absence of protoxylary canals.
6. Greater abundance of pith tissue.
7. Absence of conspicuous primary rays.

It is evident that these seven characters are neither infallible nor always useful. The centripetal development of the primary xylem is certainly distinctive in most cases but, as I have pointed out above, there is reason to believe that this was

present in some of the stems. The arrangement of the primary xylem and phloem groups is of course only of use when very young and well-preserved specimens are at hand. With reference to the third point, it is by no means easy to determine the exact anatomical origin of these organs. Judging from the few stem specimens that I have examined with roots in organic connection[3], the branch stems arise much more regularly (that is, in distinct whorls) and depart more directly than do roots. The absence of nodes appears to be a good character but of course may not be useful in a small fragmentary specimen. The absence of protoxylary canals is a striking character and a good one even though these canals are occasionally missing in the stem. Usually the roots display a solid parenchymatous pith in contrast to the central chamber of the stems; in some instances, however, the pith of the roots may be very small, consisting of a half dozen cells or less.

Renault (1885, 1896, 1898) has identified the roots of *Arthropitys* and *Calamodendron,* and although there is perhaps no reason to doubt his correlation with these stem genera no really distinctive characters are cited which would allow one to readily distinguish isolated root specimens.

Astromyelon sp.

Our Iowa specimens range up to nearly 2.5 cm. in diameter although only the xylem and pith are preserved (fig. 27). They all certainly represent one species and their intimate association with the *Arthroxylon Williamsonii* stems strongly suggests that they belong to that plant. No other calamitean stem species have been found in the collection.

Large primary rays, so characteristic a feature of most calamitean stems, are lacking (figs. 27, 28). The pith extends out into the wood (fig. 27), producing an apparently close but superficial comparison with the stem. That is, what appear to be short, broad primary rays here are clearly pith cells, and the transition at their periphery to the secondary xylem is abrupt. It is evident from the transverse section that rays are present in the secondary wood but they are for the most part only one cell wide.

The pitting in the tracheids of these roots is imperfectly preserved but when present at all it appears to consist of rather small circular pits with occasionally elongate ones in evidence. When the roots are viewed (fig. 28) in tangential section the rays are seen to be both numerous and variable in size. A ray may consist of a single small cell or of many relatively large ones, with nearly every conceivable intermediate form.

We are in need of a thorough study of the calamitean roots which will shed light on the comparative anatomy of those borne by the three stem genera considered above. With the abundance of material that is now being collected this should be possible within a very few years. There are, however, some interesting structural differences between the wood of these roots and that of *Arthroxylon Williamsonii* which may be noted.

[3] Roots have been observed with stems of *Arthropitys communis* var. *septata*, but sufficient material has not been available to make a comparison with the roots described here.

A fundamental character which appears to distinguish the two in most if not all cases is the absence of the primary rays in the roots. I feel that a distinction may be drawn between primary rays (which are so characteristic of the stems; see figs. 10, 14, 16, 29) and the pith "bays" of the roots (fig. 27). The latter may be rather deep (see, for example, Scott, 1920, fig. 16) but usually they are not and the "bay" ends abruptly. Beyond this point the wood is homogeneous, consisting of an admixture of tracheids and small rays. The general appearance approaches rather that of the peripheral region of an *Arthropitys* stem species whose primary rays tend to lose their massive identity. In general, however, the secondary wood anatomy of the stem and roots appears to be quite distinct.

If the secondary wood structures of our *Astromyelon* (fig. 28) be compared with the wood of the associated stems of *Arthroxylon Williamsonii* (figs. 19, 20) the difference is quite striking. *Astromyelon* presents a more or less uniform admixture of tracheids and small rays comparable with the wood sector of an *Arthropitys* (fig. 11). This is very different from the secondary wood anatomy of *Arthroxylon* as described above and as illustrated in figs. 19, 20.

Further speculation is not justified at present but, assuming that the roots found associated in the Iowa coal balls were borne by *Arthroxylon Williamsonii,* it would appear that the roots have retained the more normal ray structure (as displayed in *Arthropitys*), while the striking specialization of secondary tissues has been confined to the stems.

An Arthroxylon Specimen from West Mineral, Kansas.—

A specimen of *Arthroxylon* has recently turned up in our collections from the West Mineral, Kansas, locality which will be briefly mentioned here chiefly because its size is appreciably greater than that of the Iowa and Indiana specimens.

The wood attains a thickness of 18 mm. The distinction between the wood sector and primary ray is sharply defined in transverse section and remains uniform. Like in the Iowa specimens, however, the transverse view does not reveal the unique nature of the primary rays. The protoxylary canals measure about 300 μ in diameter. The wood sectors measure about 1.4 mm. wide and the primary rays about .8 mm.

In tangential section the primary "ray" cells appear to be as long as the tracheids and have essentially the same gross morphology. Occasionally, however, a vertical row of cells will be observed with transverse walls, the cells being 10–12 times as long as broad. I have observed no pitting in the walls of either of these two types of cells composing the primary ray.

The wood sector consists of tracheids which seem to be predominantly of the reticulate-bordered type with an occasional tendency toward scalariform. Scattered sparsely through the tracheids are uniseriate rays most of which are only 3–4 cells high but a few have been observed which are 2–3 times as tall as that. The component cells are variable in size and shape. They tend to be squarish or vertically elongate, and may vary in a single ray from 84 $\times$ 48 μ to 350 $\times$ 50 μ, the first dimension in both cases being the vertical one.

Acknowledgment.—

This study was carried out during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation. I wish to express my appreciation for aid received from the Foundation and for the facilities placed at my disposal by the Botanical Museum, Harvard University.

Grateful acknowledgment is also made to Mr. Frederick O. Thompson, of Des Moines, Iowa, for defraying in part the cost of the plates.

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Explanation of Plate

PLATE 18

Arthropitys communis (Binney) Hirmer & Knoell, var. *septata* Andrews

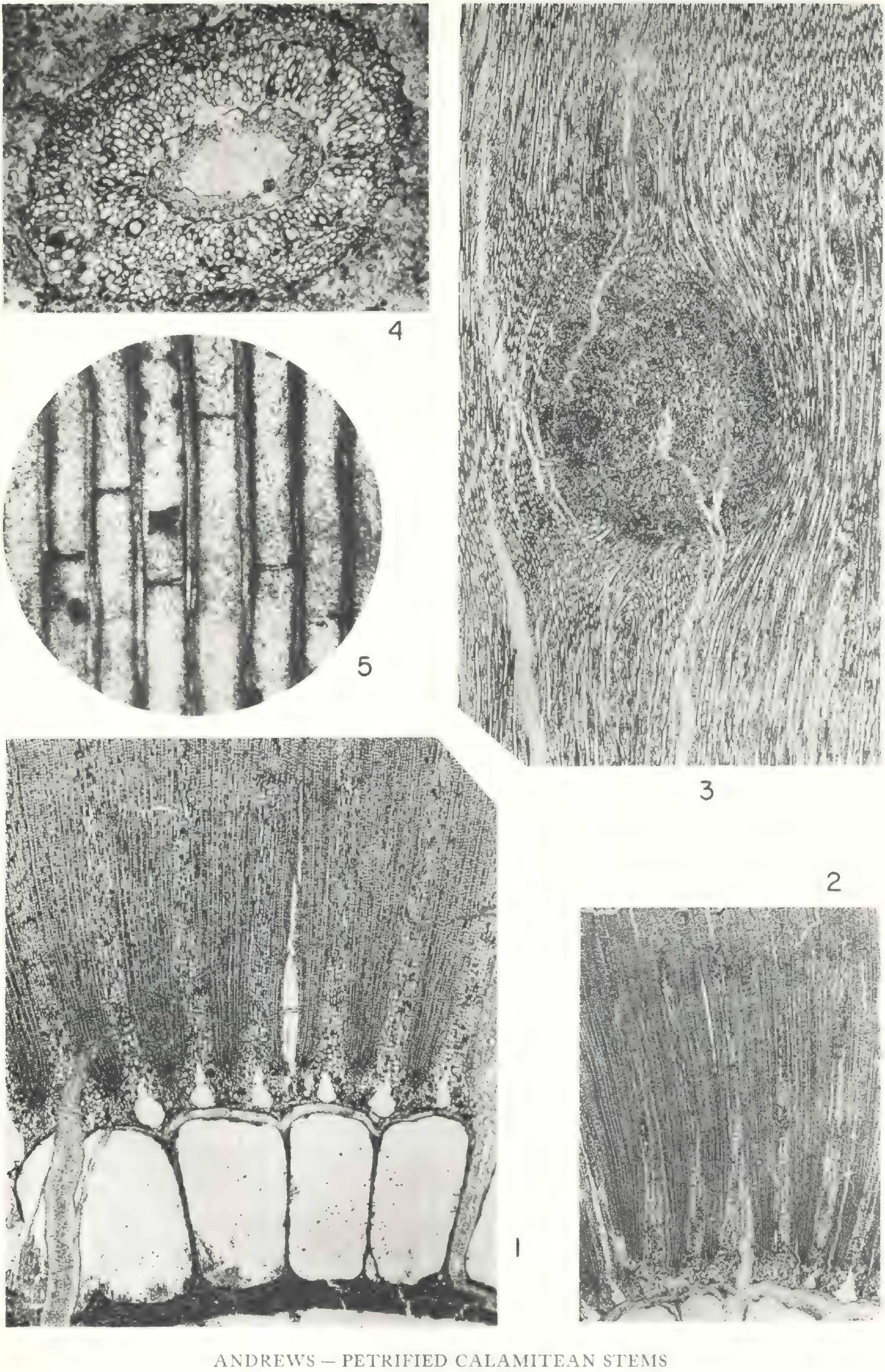
Fig. 1. Inner portion of the wood and peripheral pith region in transverse section. Coal ball No. 722. Peel 722-C4-1. × 9.

Fig. 2. Transverse section of a portion of the stem showing the extent of secondary growth. Coal ball No. 722. Peel 722-C4-20. × 5.

Fig. 3. Tangential section showing a departing branch stele. Coal ball No. 722. Peel 722-C5a-4. × 10.

Fig. 4. A small stem from the Berryville, Illinois, locality, possibly referable to *A. communis* var. *septata.* Slide 1969. × 32.

Fig. 5. Tangential section of a wood sector near the pith showing the septate nature of the tracheids. Coal ball No. 722. Slide 1931. × 140.



ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 19

Arthropitys communis (Binney) Hirmer & Knoell, var. *septata* Andrews

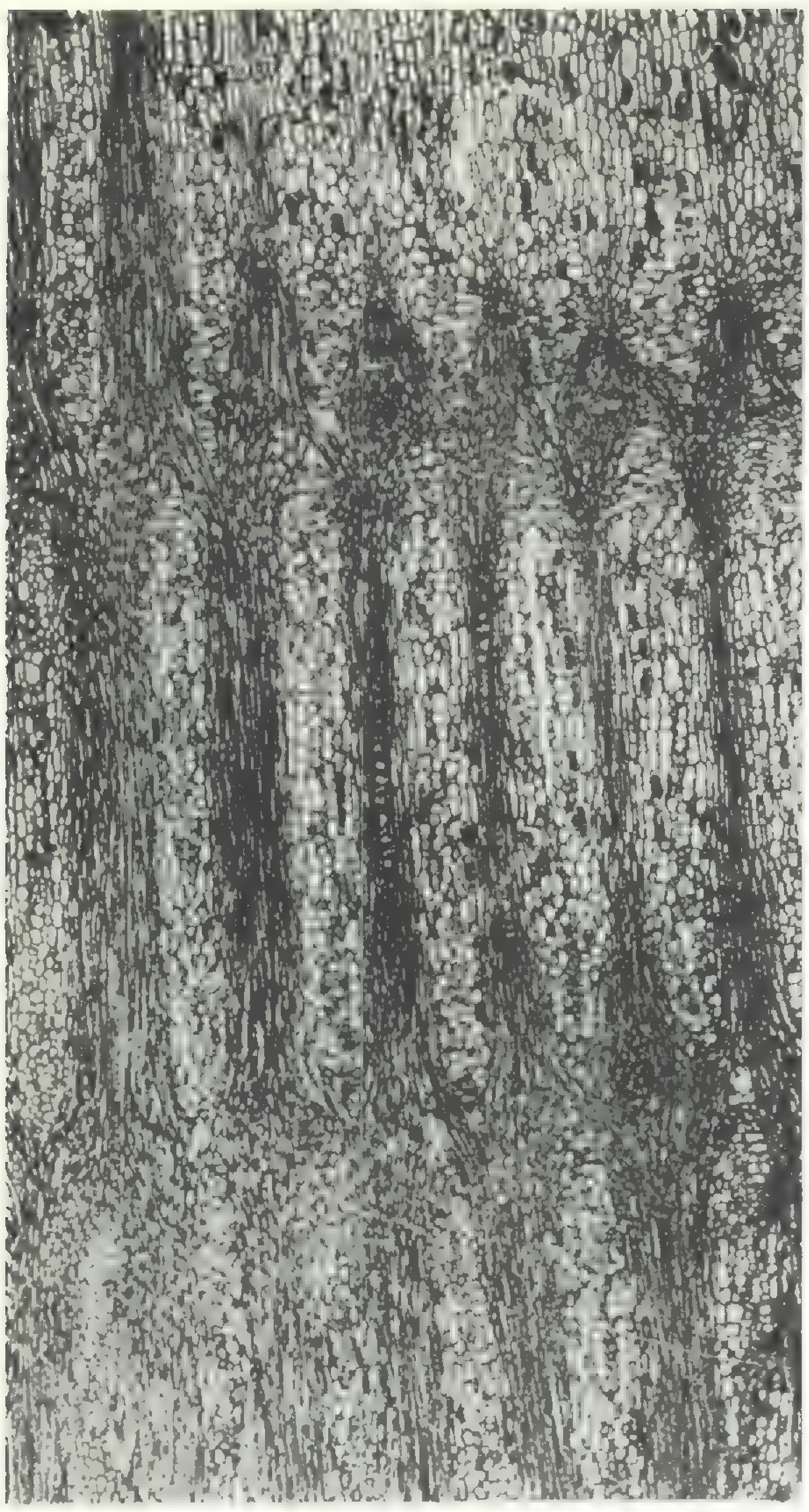
Fig. 6. Tangential section of stem near pith. Coal ball No. 722. Peel 722-C2-15. × 9.

Fig. 7. Tangential section of stem several mm. from the pith (see text). Coal ball No. 722. Peel 722-C2-2. × 9.

Fig. 8. Scalariform pitting in radial walls of tracheids. Coal ball No. 722. Slide 1931. × 145.

Fig. 9. Radial view of secondary ray in wood sector. Coal ball No. 722. Slide 1931. × 46.

Fig. 10. Portion of stem in transverse section. Coal ball No. 804. Slide 1948. × 13.



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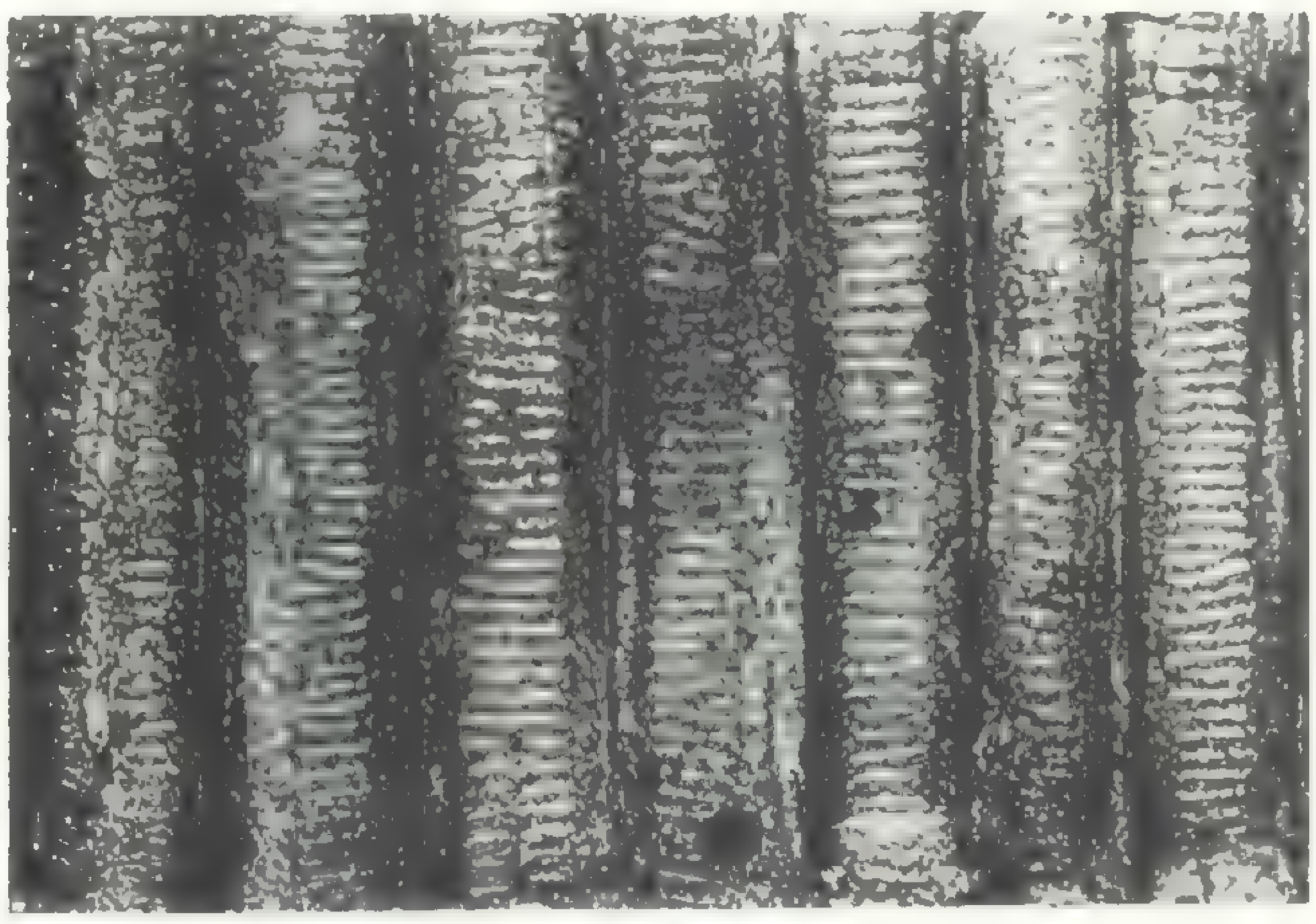

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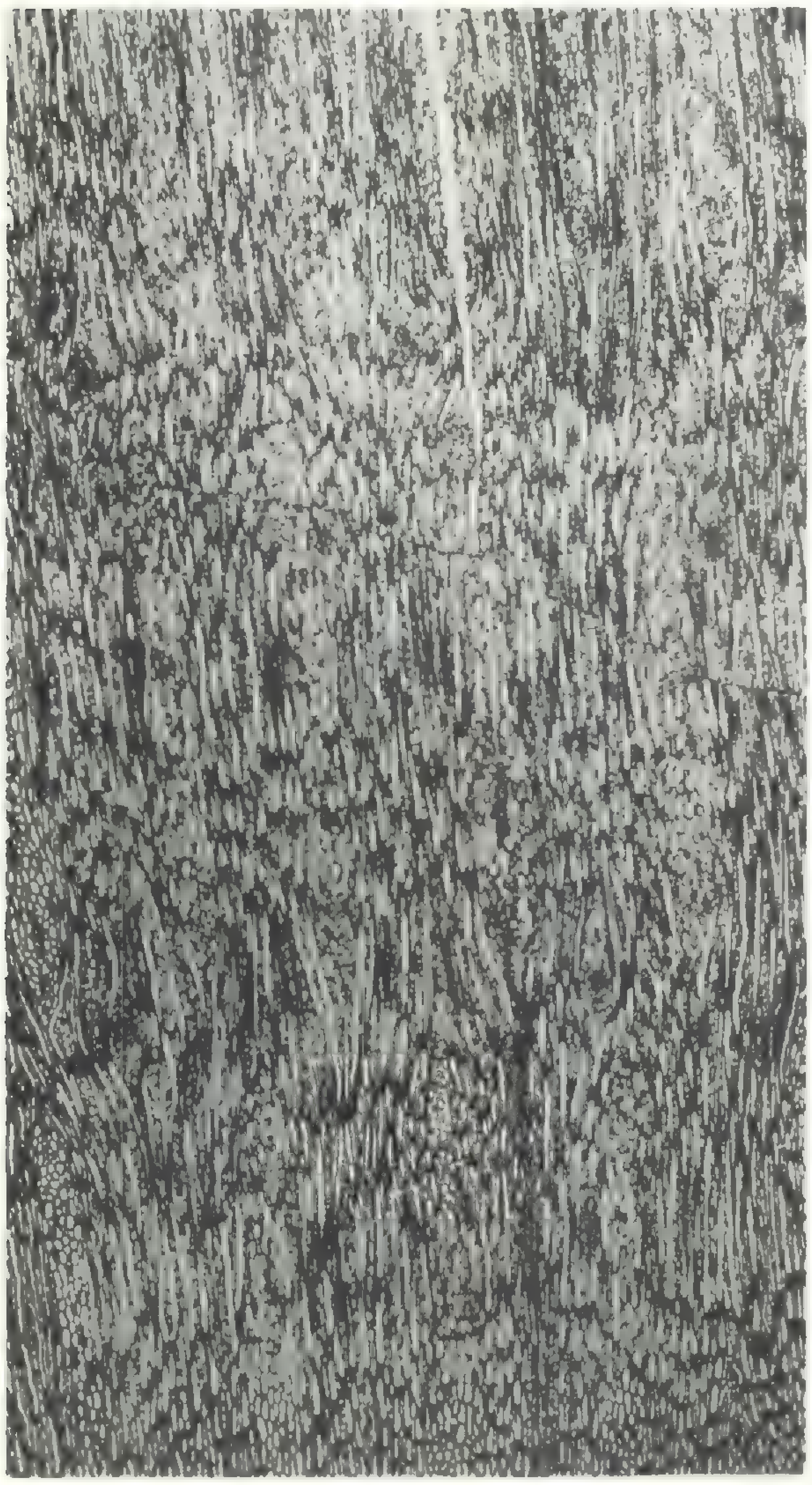

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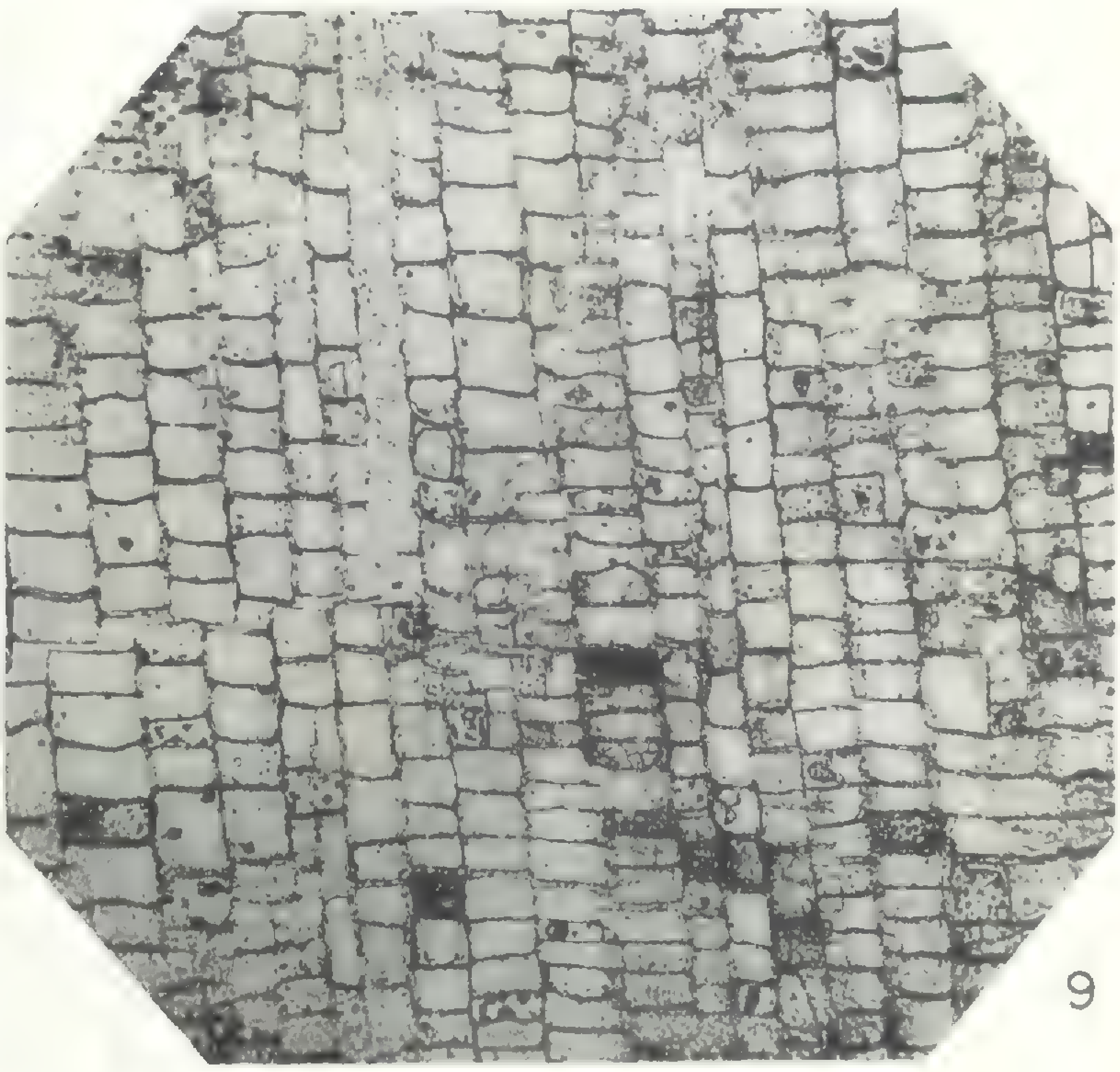

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ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 20

Arthropitys kansana Andrews

Fig. 11. Tangential section showing two narrow primary rays. Coal ball No. 786. Slide 1920. × 34.

Fig. 12. Pitting in radial walls of tracheids. Coal ball No. 786. Slide 1921. × 110.

Arthropitys communis var. *septata* Andrews

Fig. 13. A small stem from the locality of Berryville, Illinois. Slide 1968. Coal ball No. 756. × 20.

Fig. 14. A portion of the stem in transverse section. Coal ball No. 755. Peel 755-A-b2. × 7.

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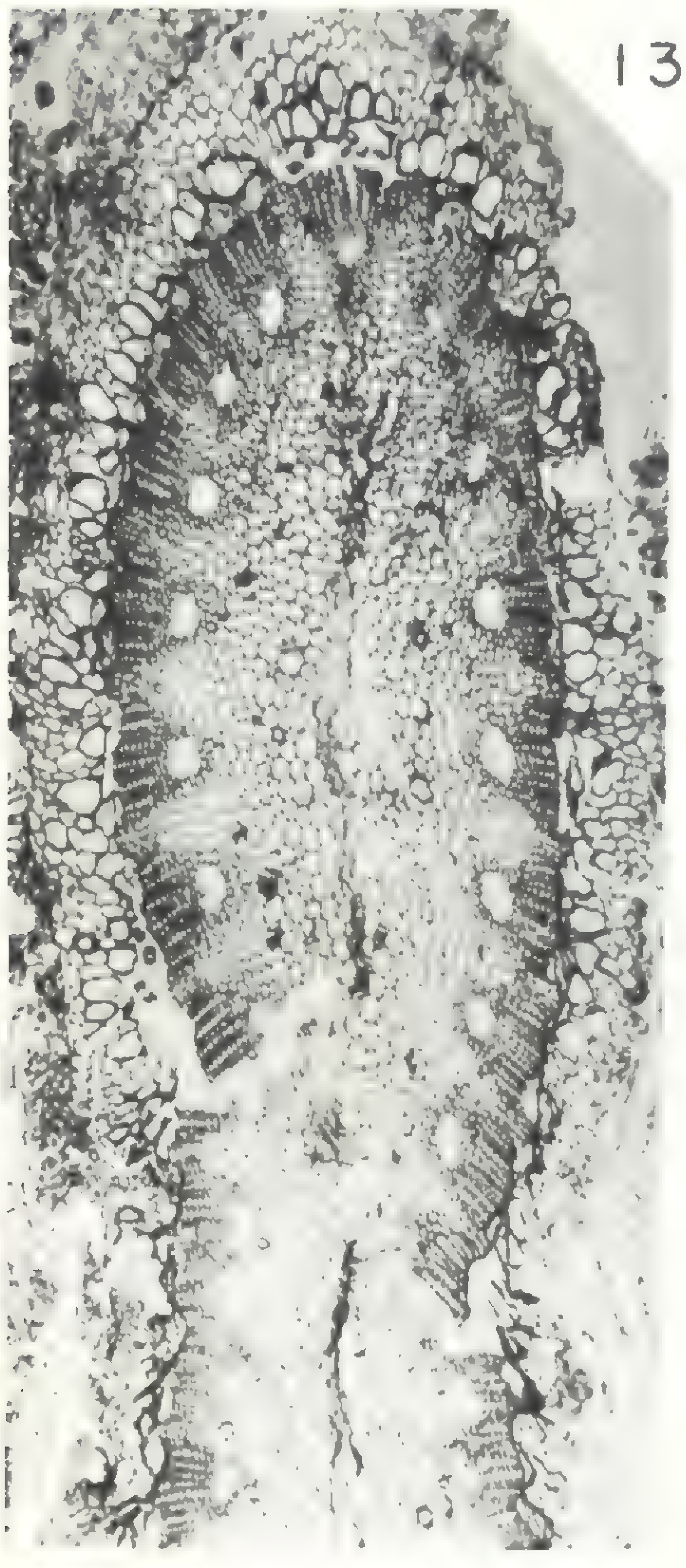

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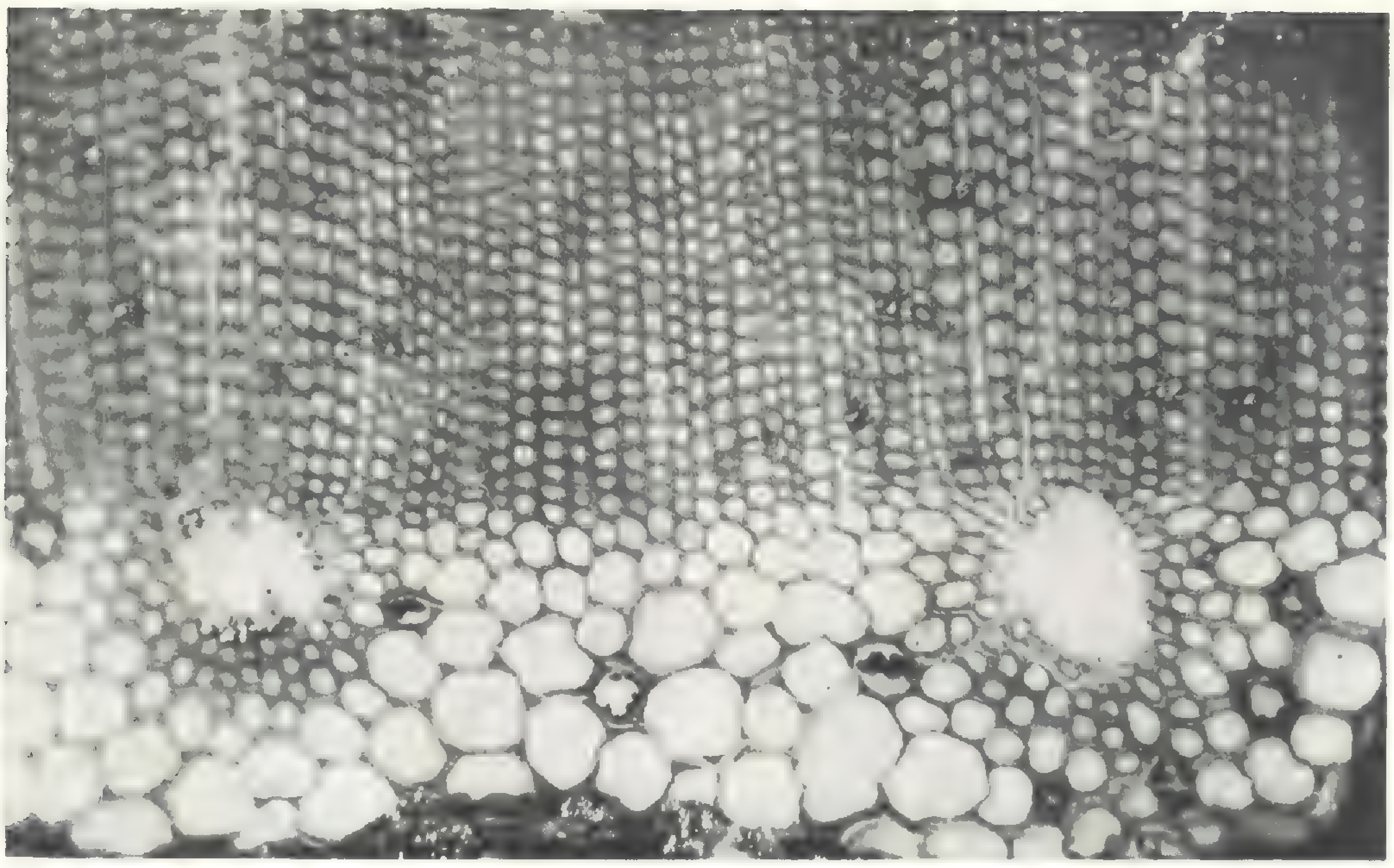
ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 21

Fig. 15. *Arthroxylon Williamsonii* Reed. A portion of the stem in transverse section. Coal ball No. B30. Slide 1972. × 60.

Fig. 16. *Arthropitys* sp. A. A portion of the stem in transverse section. Coal ball No. 805. Slide 1955. × 14.



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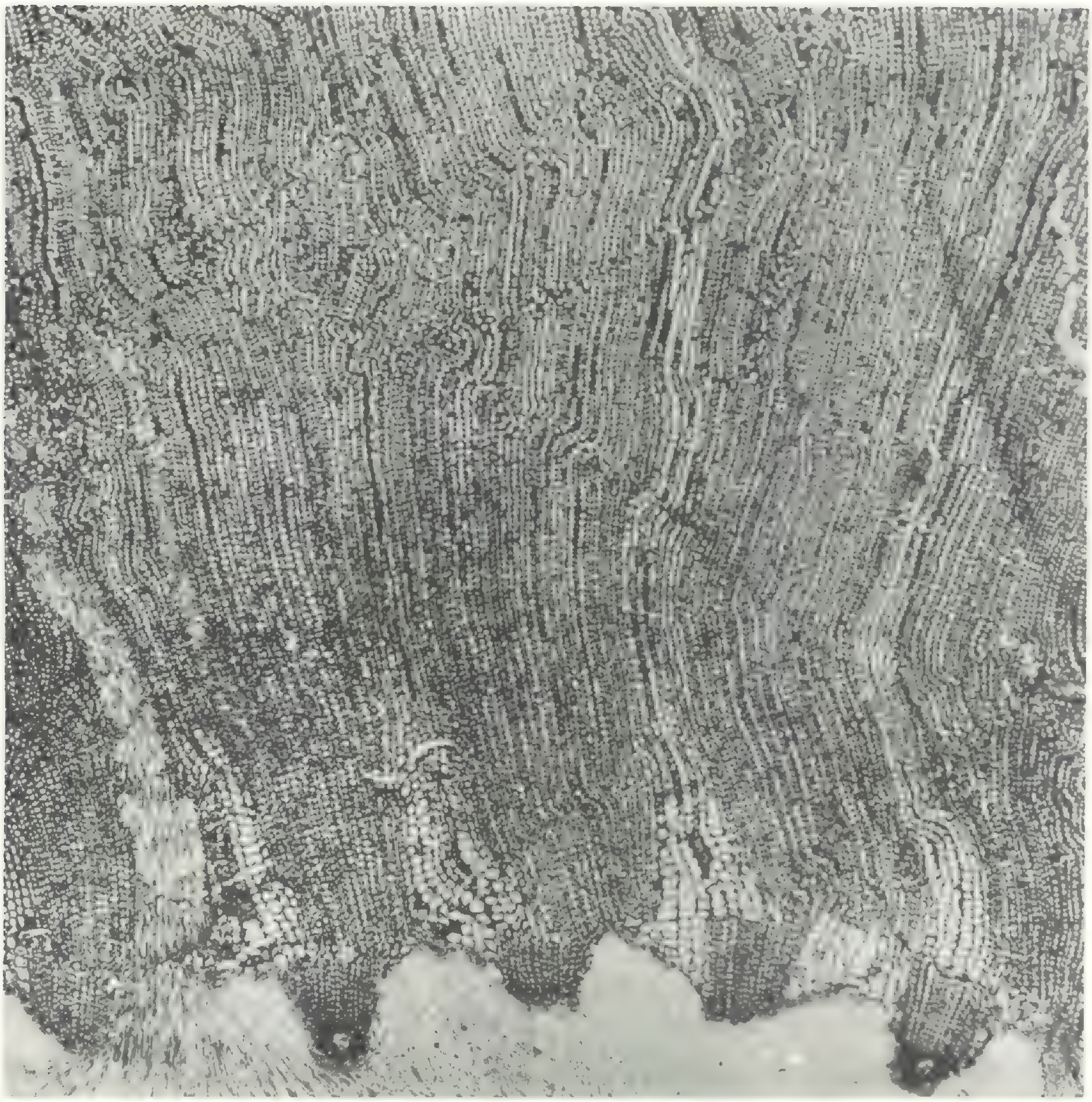

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ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 22

Fig. 17. *Arthropitys kansana* Andrews. Tangential section of the wood enlarged showing one primary ray and numerous secondary rays in the wood sector. Coal ball No. 786. Slide 1920. × 50.

Arthroxylon Williamsonii Reed

Fig. 18. Radial section of a secondary ray of the wood sector. Coal ball No. B3. × 65.

Fig. 19. Tangential section of the stem showing a primary ray (dark) with portion of a wood sector on either side. Coal ball No. B3. Slide 1973. × 60.

Fig. 20. A wood sector in tangential section showing the vertically elongate nature of the secondary ray cells. Coal ball No. B3. Slide 1973. × 74.

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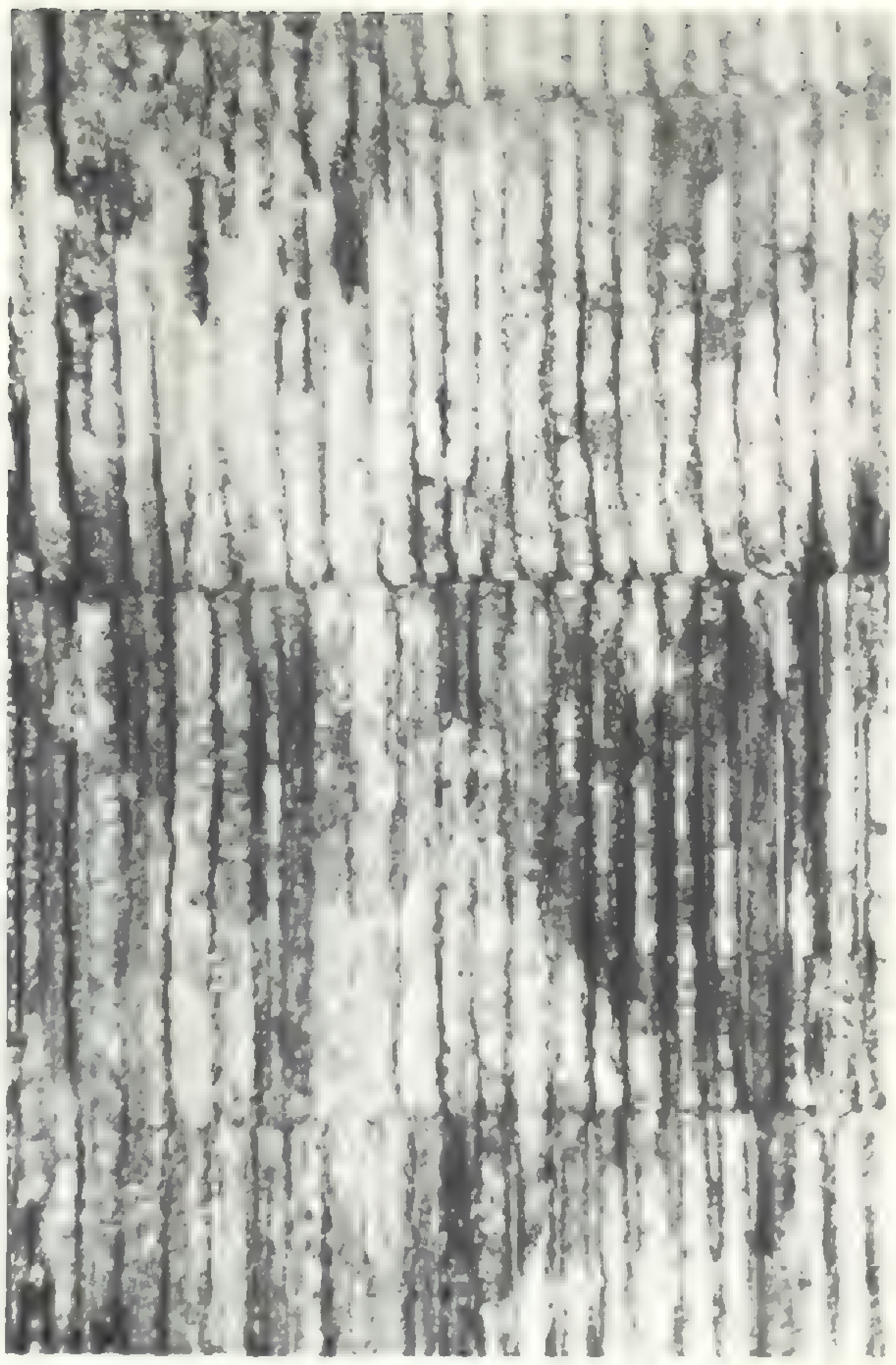

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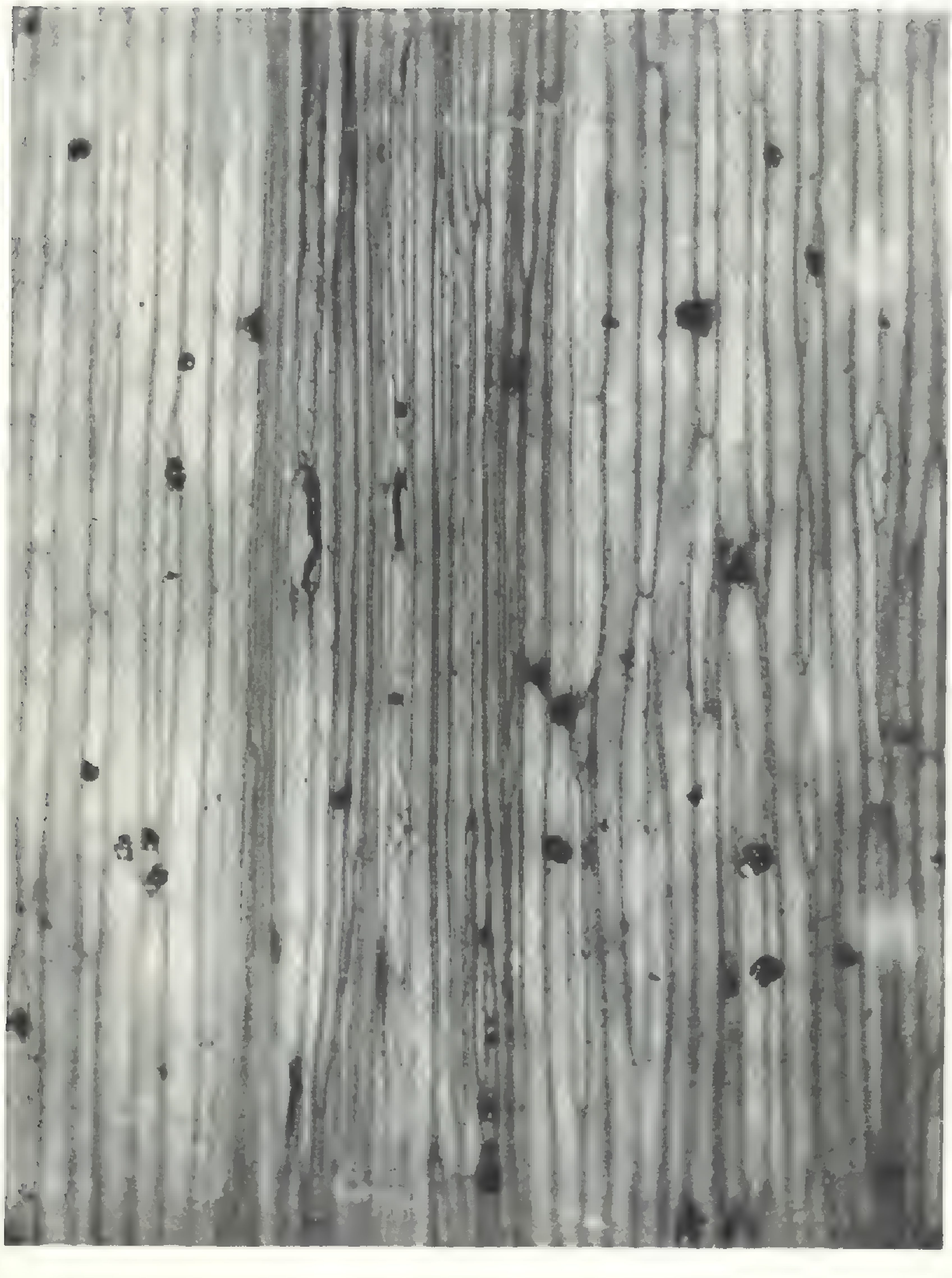
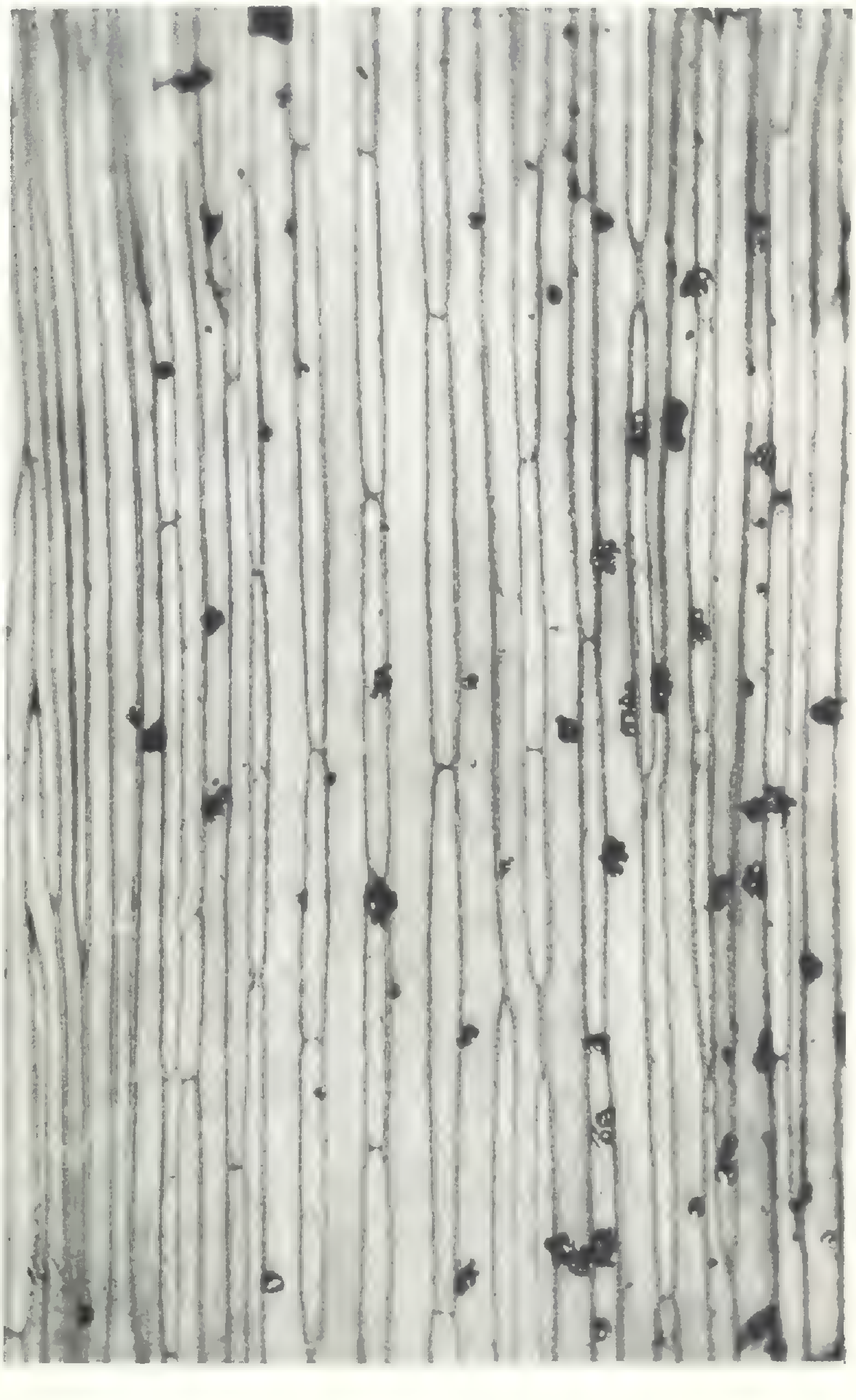




ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

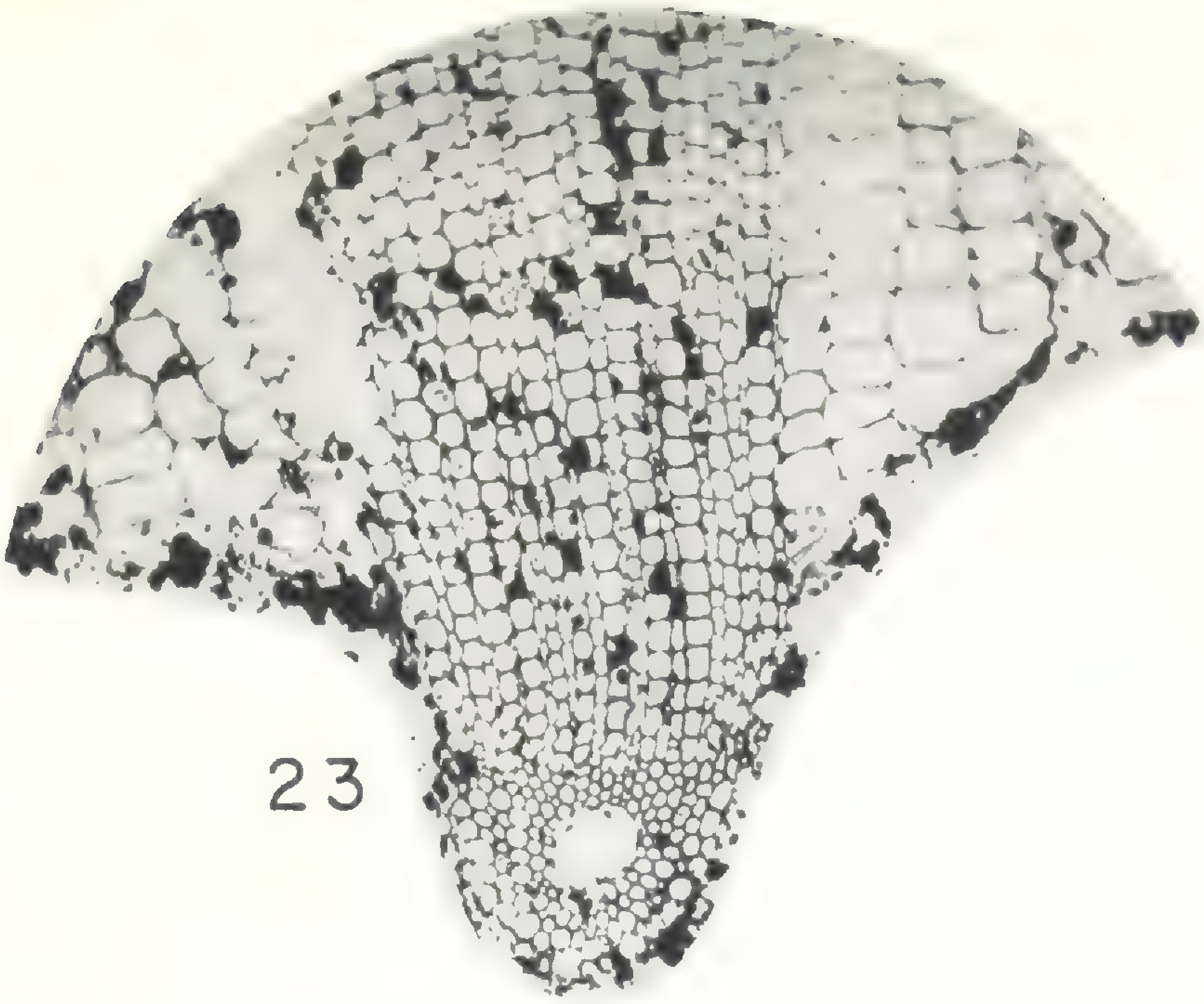
PLATE 23

Figs. 21, 22. *Arthropitys* sp. B. Pitting in radial walls of tracheids. Coal ball No. 753. Slide 1924. × 175.

Figs. 23, 24. *Arthropitys* sp. A. Showing thick-walled cells (centripetal tracheids?) on inner side of protoxylary canal. Coal ball No. 805. Slide 1955. × 40.

Fig. 25. A single protoxylary group of the root shown in fig. 27. Coal ball No. B30. Slide 1942. × 37.

Fig. 26. *Arthropitys kansana* Andrews. Radial view of secondary ray of wood sector. Coal ball No. 755. Slide 1915. × 50.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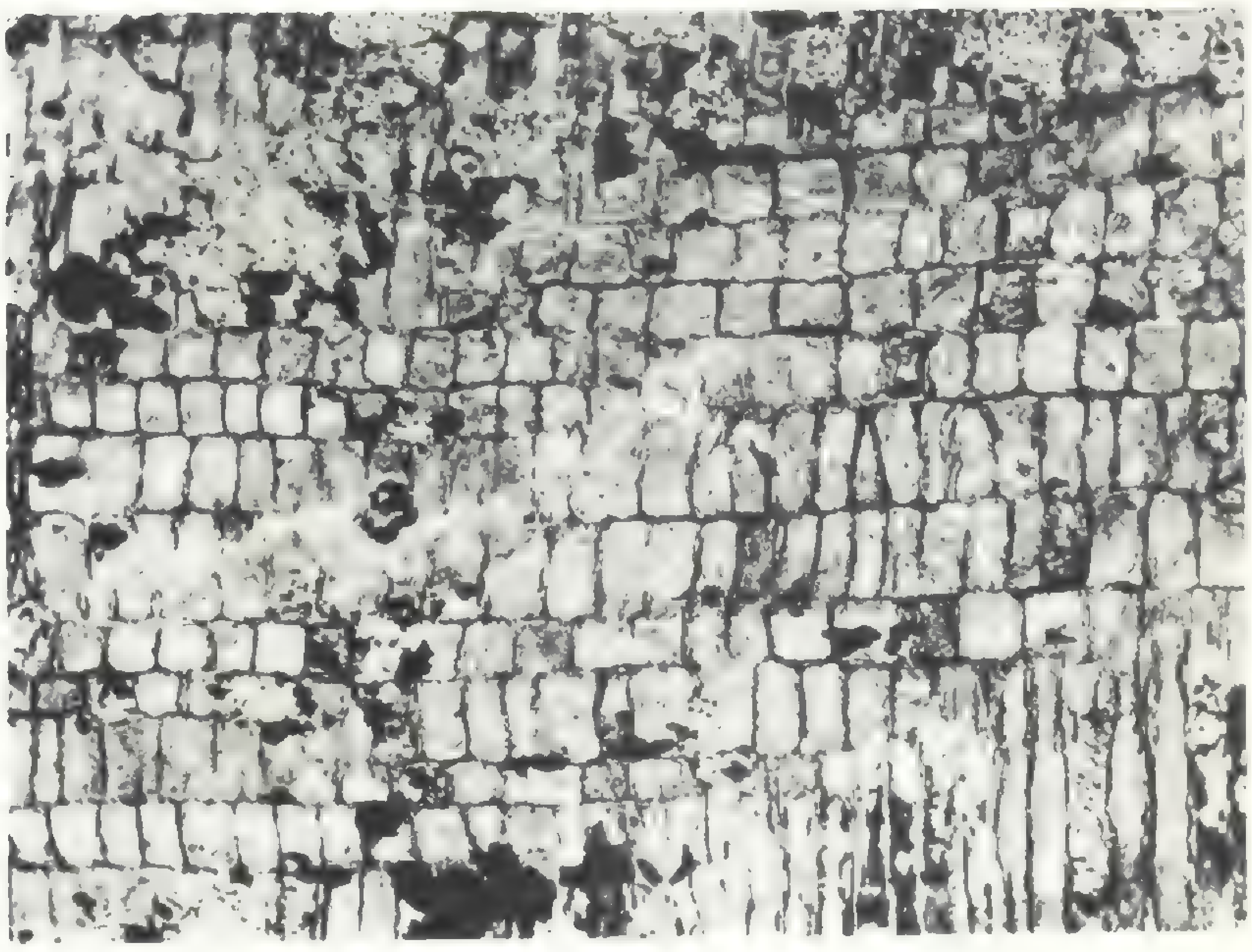

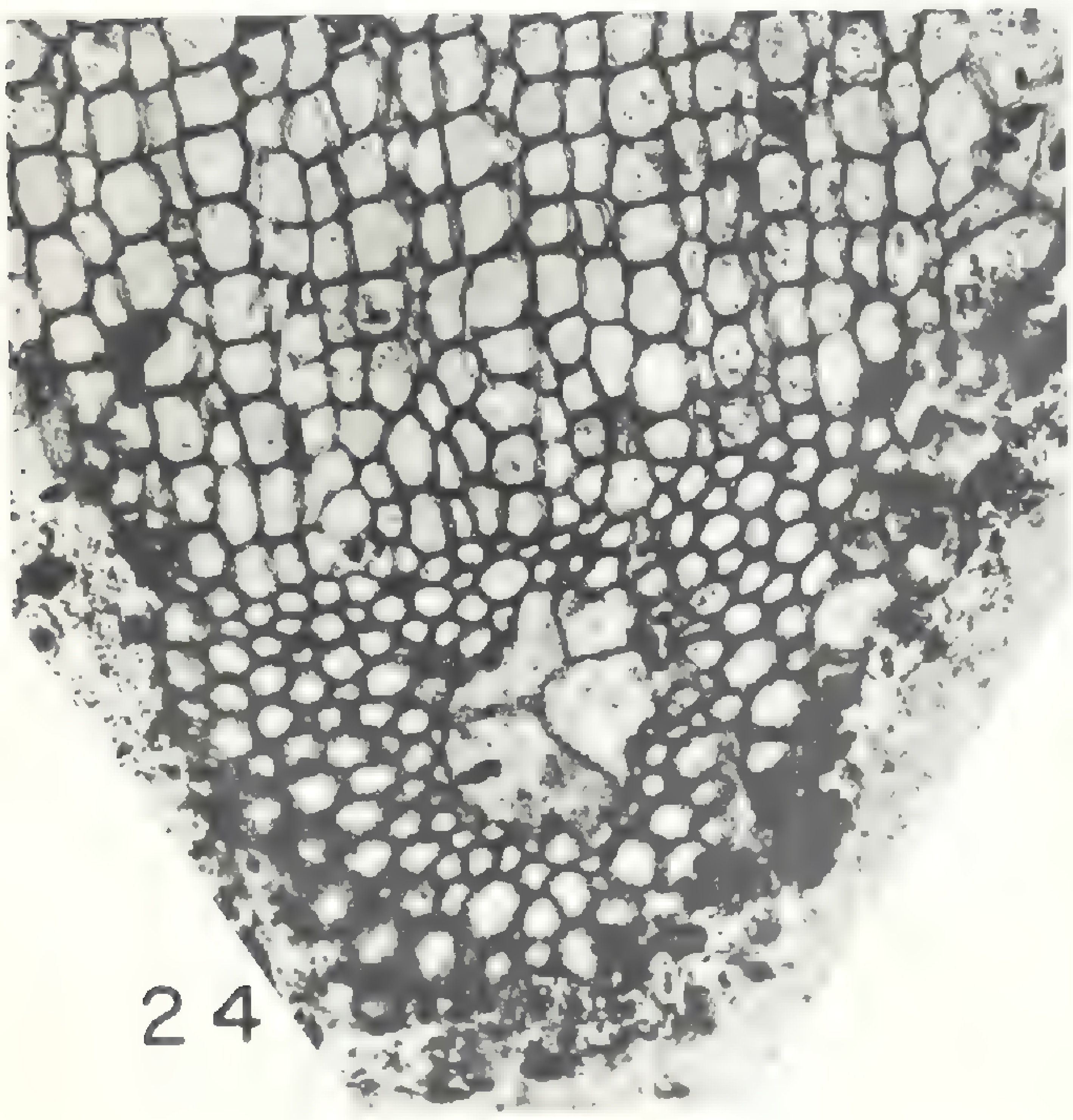
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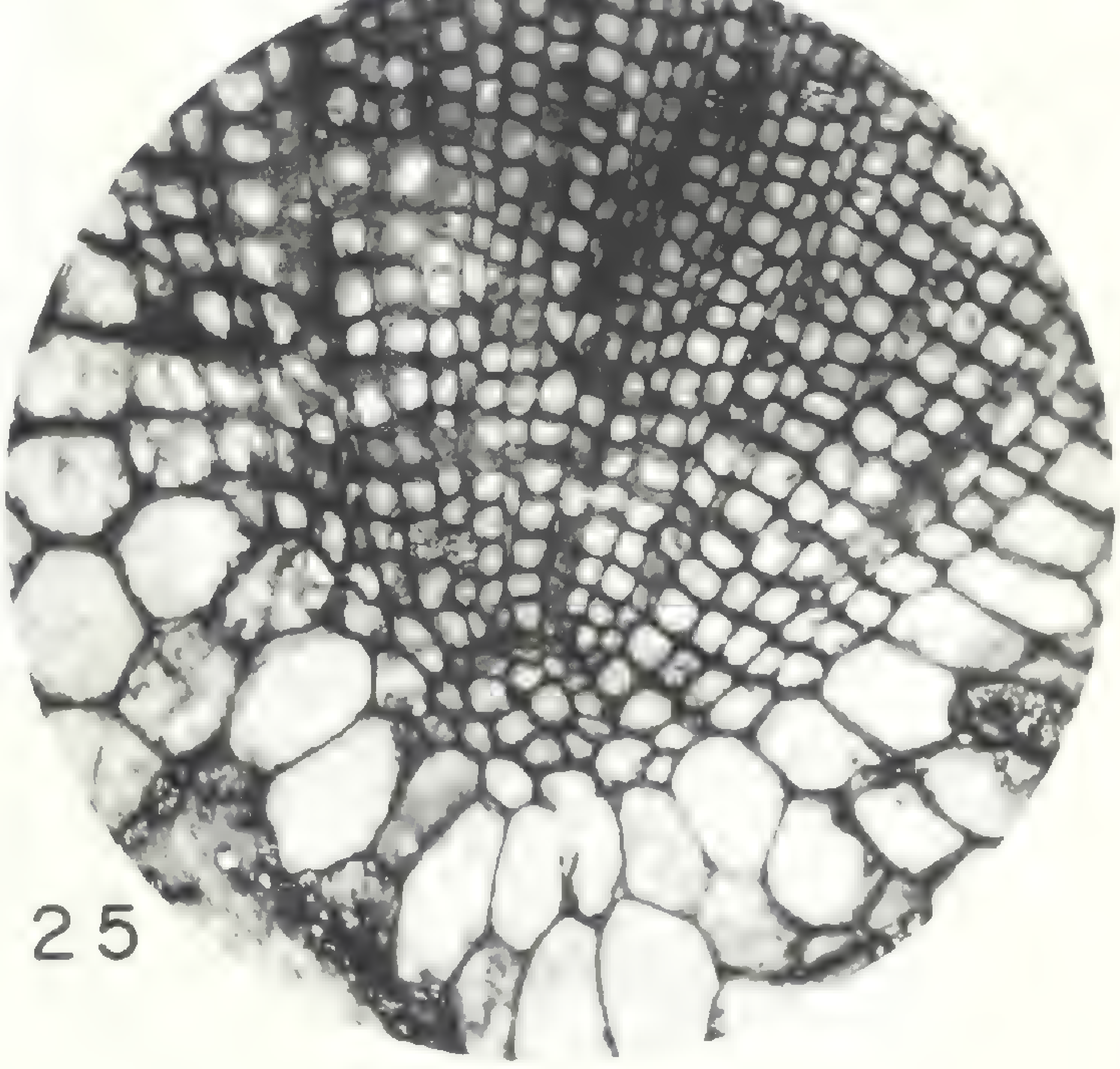
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ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 24

Astromyelon sp., probably root of *Arthroxylon Williamsonii* Reed

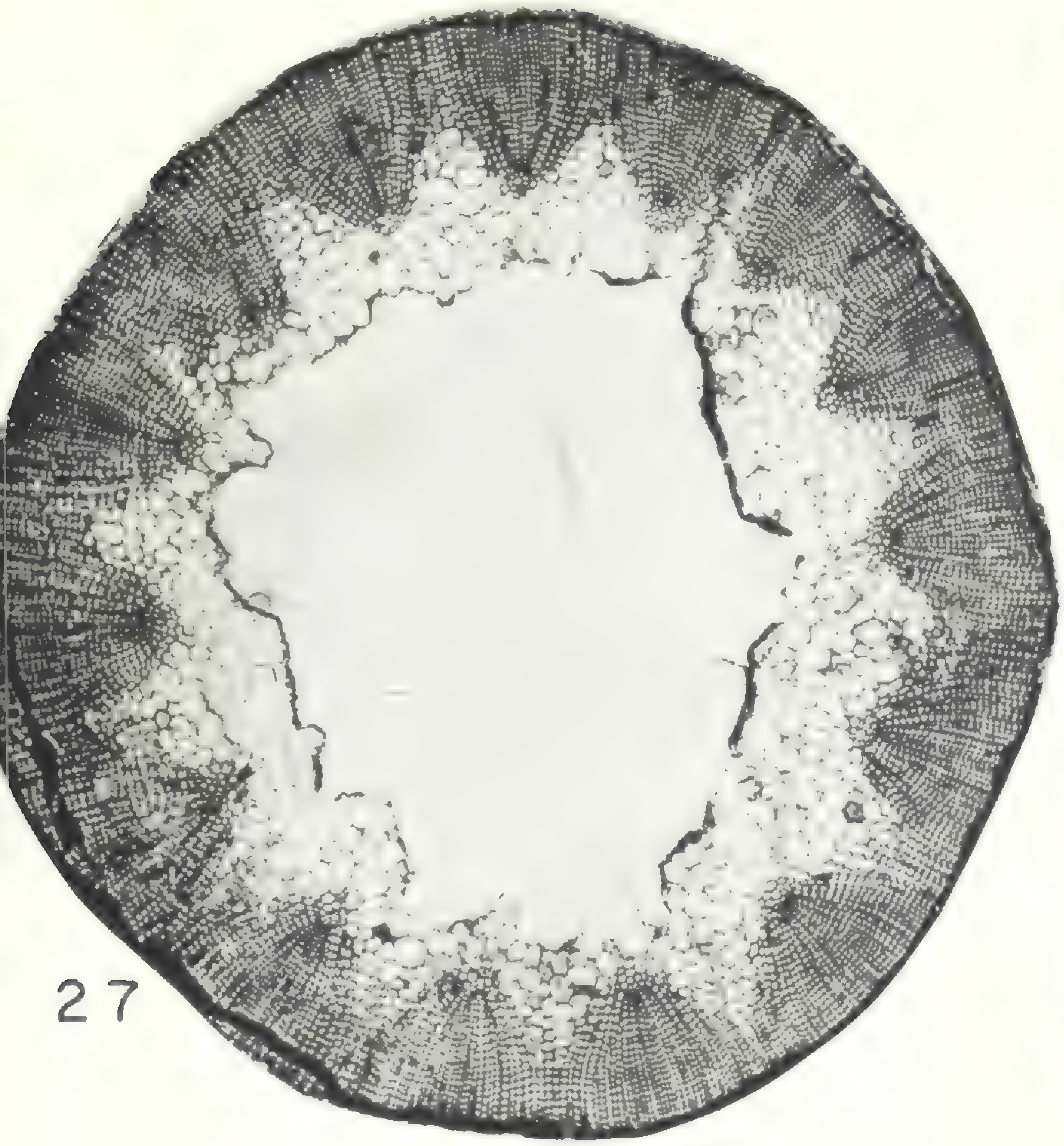
Fig. 27. Transverse section. Slide 1942. × 7.5.

Fig. 28. Tangential section. Slide 1976. × 16.

Calamodendron americanum Andrews

Fig. 29. Transverse section. Peel 709-B-t 6. × 11.

Fig. 30. Tangential section showing a primary ray flanked by the fibrous cells characteristic of this genus. A fiber cell may also be noted running through the middle of the ray. Slide 1913. × 100.



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ANDREWS — PETRIFIED CALAMITEAN STEMS

VARIATION IN THE PERFOLIATE UVULARIAS*

ROBERT A. DIETZ**

In New England and New York, where the two perfoliate species of *Uvularia* are found, little difficulty is encountered in distinguishing them. Although both species in that area vary somewhat, *U. perfoliata* is small and glabrous, while *U. grandiflora* is distinctly larger and its leaves are pubescent on the lower surface. However, southward along the western border of the distribution of *U. perfoliata*, the variation within both species becomes so marked that for occasional collections the accepted criteria for distinguishing them breaks down. In the perfoliate species of *Uvularia*, variants more or less difficult to classify are most commonly found along a line roughly extending from Rochester, New York, down the Appalachian Mountains through eastern Tennessee and into northeastern Alabama. For example, while the New England botanist could tell at a glance the species to which a plant from the Berkshires belonged, he would require a hand-lens for classifying them in eastern Tennessee, and even with this aid several plants from a given woodland would probably be termed "special problems."

In order to measure this perplexing variation and to analyze its cause, the present project was undertaken. Mass collections of plants of *Uvularia perfoliata* and *U. grandiflora* were obtained from several collaborators, as listed below,[1] and they were supplemented by further collections made during the course of the investigation. Individuals from these mass collections were measured, the measurements covering the following characters:

- Pubescence
- Length of longest internode
- Number of leaves
- Number of fruits
- Leaf index (leaf width/leaf length)
- Leaf length
- Leaf width
- Leaf shape
- Length of first internode below branch
- Length of second internode below branch
- Length of third internode below branch
- Length of first internode, fertile branch
- Length of first internode, sterile branch
- Ratio of first internode on fertile branch to first internode on sterile branch
- Length of each additional internode, sterile branch
- Length of each additional internode, fertile branch
- Shape of fruit
- Length of fruit pedicel
- Number of hairs per square millimeter on lower leaf surface
- Length of hairs on lower leaf surface

Wherever the nature of the material permitted, these measurements were treated statistically. The method of pictorialized scatter diagrams was chosen to analyze these data, since it permits several variables to be depicted on a single chart

[1] Edgar Anderson, Missouri Botanical Garden; Reino Alava, Missouri Botanical Garden; Ralph Erickson, University of Pennsylvania; Norman Fassett, University of Wisconsin; Leslie Hubricht, Danville, Virginia; Royal Shanks, University of Tennessee; Stanley Smith, New York State Museum; George Van Schaack, Washington University; H. A. Wallace, South Salem, New York; and Edgar Wherry, University of Pennsylvania. In addition, material was examined in the following herbaria: Cranbrook Institute of Science, Missouri Botanical Garden, New York Botanical Garden, University of Michigan, and University of Pennsylvania.

*An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the degree of Doctor of Philosophy.

**Department of Botany, University of Tennessee, Knoxville.

rather than two, as in ordinary scatter diagrams. The first five characters in the above list were finally adopted for the charted data.

Mature plants were used in all measurements. A plant was considered mature when it had ceased elongating and the terminal leaves were fully expanded. This occurs at some time after the fruit has developed to a point where its mature form is clearly recognizable, two to three weeks after the perianth has fallen off. Depending on the clone and the environment, this may be from late April to mid-June. The plants remain in a "measurable" state from this time until the first autumn frost, except for the fruits, which reach full size about two months after the perianth has fallen.

Since plants in flower have not reached maximum growth, floral characteristics do not appear in the above list, but some discussion of floral characteristics is given later in this paper.

General Characteristics of the Perfoliate Uvularias

The perfoliate species of *Uvularia* constitute a natural division of the genus, and consist of two species, *U. perfoliata* and *U. grandiflora*. These are plants with a short rhizome containing numerous fleshy appendages, an aerial stem bearing

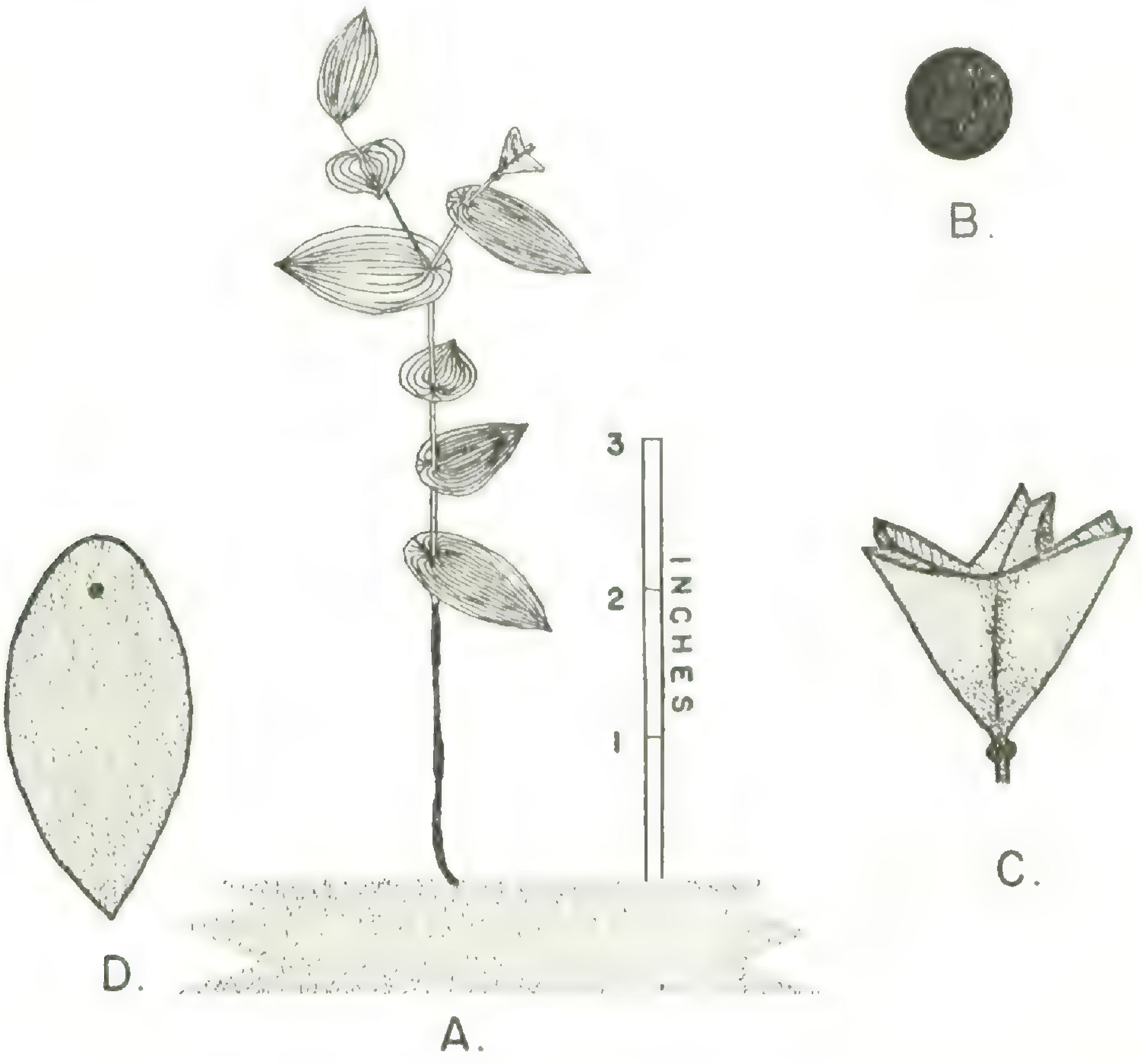


Fig. 1. *Uvularia perfoliata:* A, habit; B, dot as used on charts; C, fruit; D, leaf outline (× 2 habit scale).

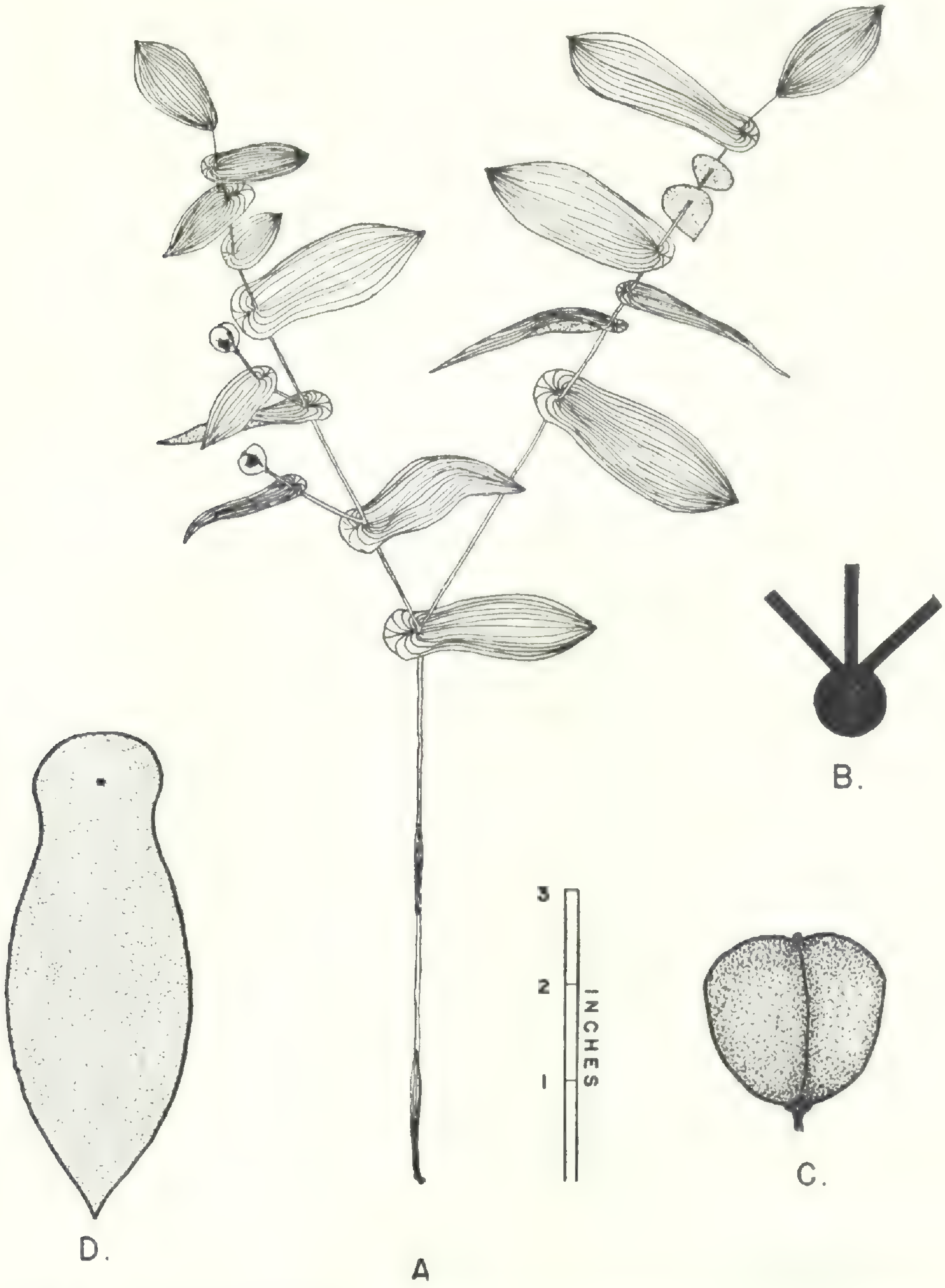
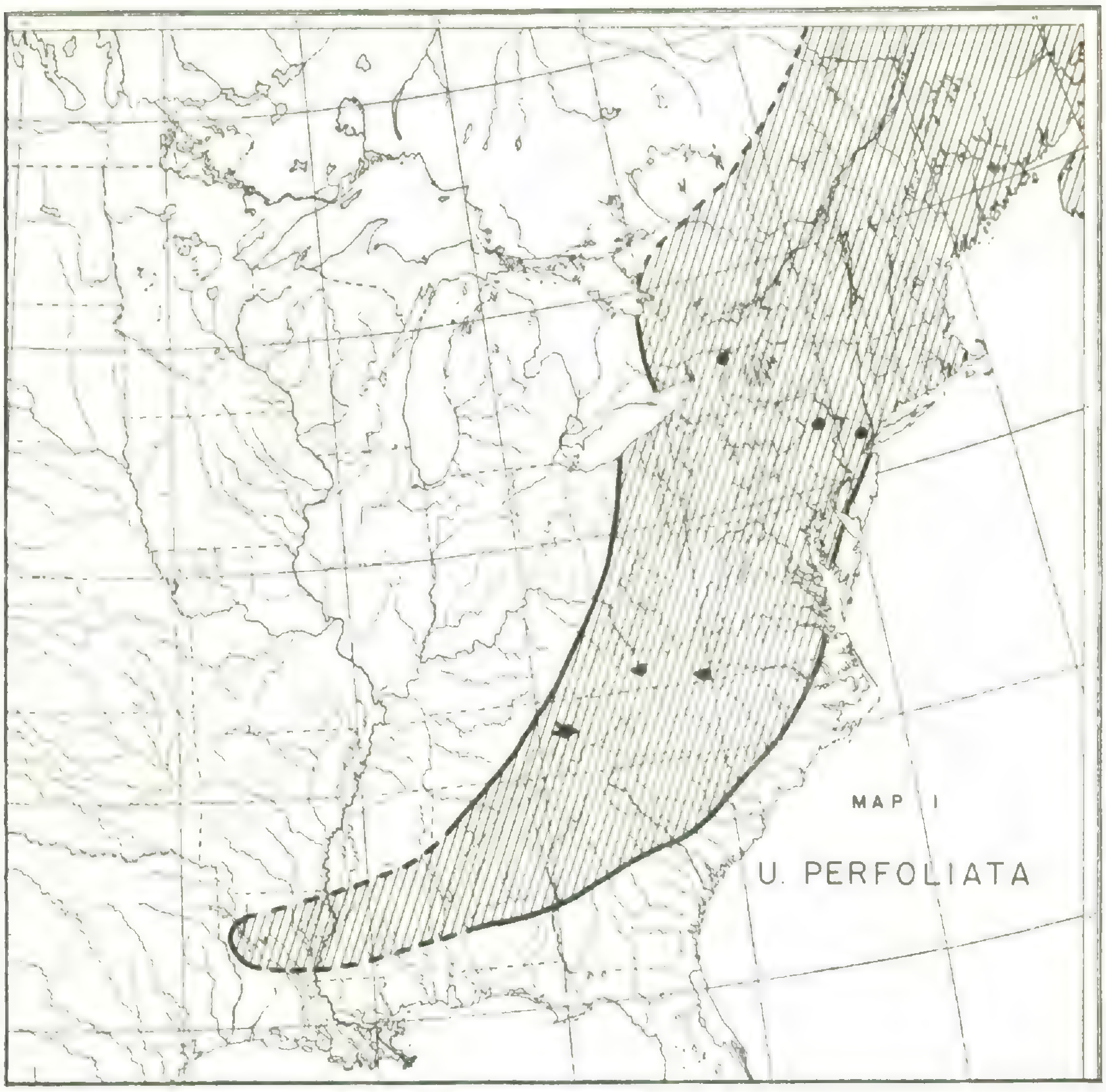


Fig. 2. *Uvularia grandiflora:* A, habit; B, dot as used on charts; C, fruit (about × 4 habit scale); D, leaf outline (×2 habit scale).

3–5 cataphylls below and 6–36 perfoliate leaves above. Mature plants characteristically are branched one or more times, the branching superficially resembling a true dichotomy. One to four flowers may be present on a given aerial stem. These are axillary, and are never borne below the lowest branch. The liliaceous perianth is made up of three yellow petals and three yellow sepals. The flowers droop, never developing the widely spreading perianth segments characteristic of such genera as *Lilium* or *Hyacinthus.* Flowering occurs within a few days to about

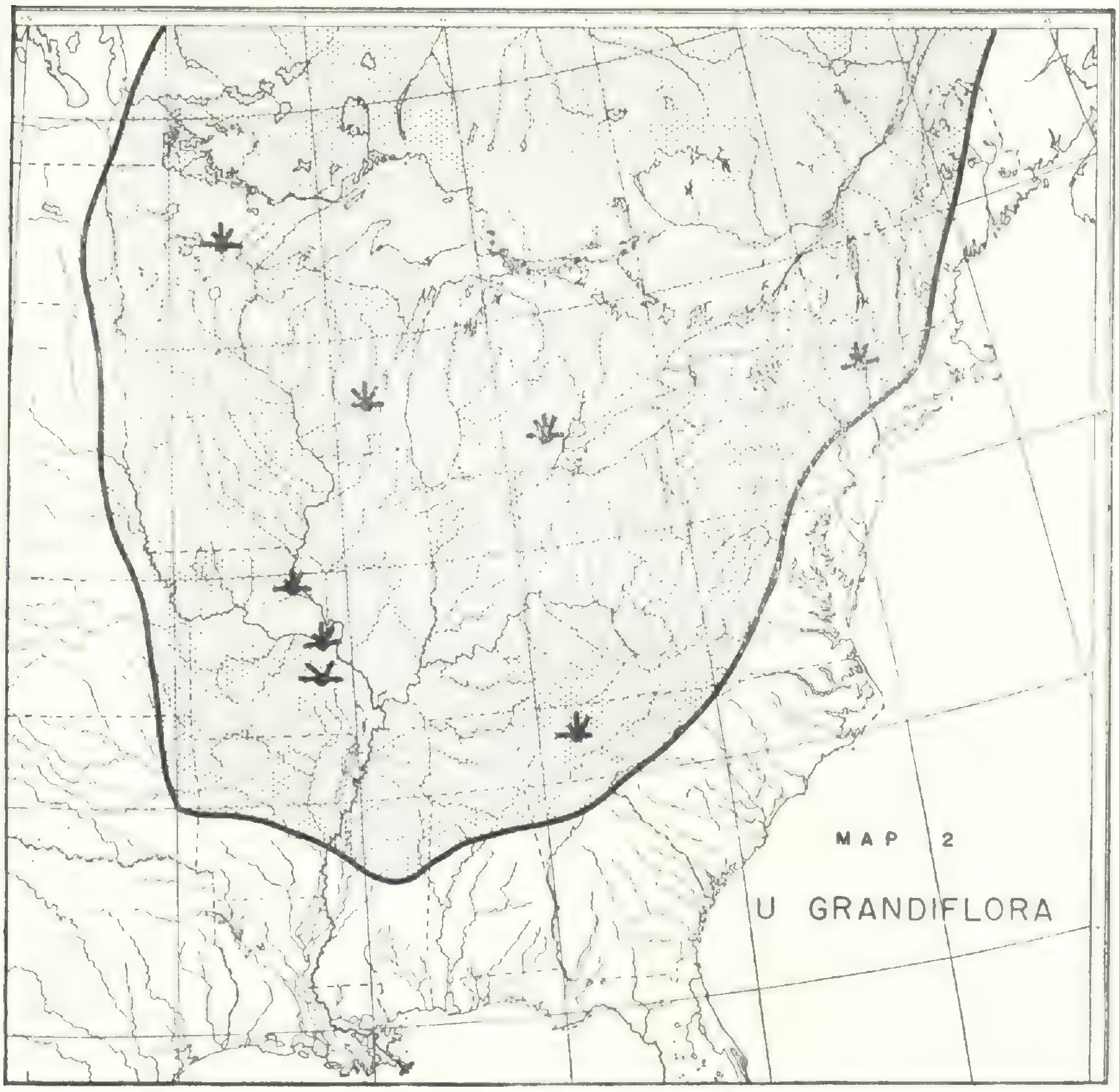


The symbols used on Maps 1 and 2 are similar to those on the charts. An additional pair of rays depicts the values found on the ordinate and abscissa, the ray to the left depicting the longest internode with increasing values to the left; that on the right, the leaf index with increasing values to the right.

a week after the first shoot appears above the ground and consequently before the plants have reached full size. Statistically useful data on vegetative parts of the plant are impossible at this stage. The 3-angled loculicidal fruit contains about 12 round, dark, hard seeds 2–3 mm. in diameter. The capsule shape varies from sharply acute at the tip to moderately obtuse and lobed (fig. 5).

Uvularia perfoliata and *U. grandiflora* are woodland plants, varying in their preference for deep or open situations, soil types, and plant associations. The plants usually persist from mid-spring to mid-autumn. Maximum growth on the aerial stems has occurred shortly after the fruits are large enough to be recognized. The plants used for measurements of vegetative parts in this project were all mature, in the sense that maximum growth had been reached.

Having considered the characteristics of the perfoliate Uvularias as a whole, the intraspecific characters will now be discussed.



Uvularia perfoliata.—This species was established in the first edition of Linnaeus' 'Species Plantarum,' in 1753. It is a small plant, with 5 to 8 leaves of which 3 or 4 are below its single branch. The leaves are glabrous, glaucous, oval and thin; the one subtending the branch is 65 mm. or less long. The longest stem internode, generally found below the lowest leaf, is 100 mm. or less long. The flower-bearing branch has a single leaf that subtends the flower. The single flower is pale yellow. The perianth segments have a granular appearance on the inside caused by rough, many-celled emergences. These are visible to the unaided eye, and under the hand lens are shown to be small papillae. The 6 stamens are as long or shorter than the trifid style. The tips of the anthers are pointed. The three-angled capsule of the fruit is broader than long (each angle two-ridged), the tip acute (fig. 1C).

Uvularia perfoliata is found in rather open woods, in neutral or slightly acid soil, frequently under white oaks and rarely under red oaks. Our collecting experience has been that the species was never particularly abundant in the mature form. Seedlings and sexually immature, non-branching older plants are not uncommon in many white oak woods, but these are nearly useless for comparative purposes.

Uvularia grandiflora.—James E. Smith, the British botanist, described this species in his 'Exotic Botany' in 1804. It is a considerably larger plant than *U. perfoliata,* sometimes waist-high. There is a single leaf below the lowest branch. Generally there are 16 or more leaves on the plant, and there may be as many as 36. These are pubescent below, dark green, thicker than those of *U. perfoliata* and frequently shaped like a "Dutchman's shoe" (fig. 2D). The leaf subtending the branch is 85 mm. or more long, typically 100–130 mm. long. The longest stem internode, generally found below the lowest leaf, is 150 mm. or longer. Flowers may be borne on either the main branch, or on secondary or tertiary side branches, and generally number from 1 to 4. The branches are leafy. The flowers are yellow, somewhat brighter than those of *U. perfoliata.* The perianth segments are smooth on the inside. The 6 stamens are longer than the style, with blunt-tipped anthers. The three-angled capsule of the fruit is obtusely lobed at the tip (fig. 2C).

Uvularia grandiflora usually grows in deep woods, in beech-maple forests or in oak-hickory forests, and there is no apparent preference for red or white oaks. It is generally found abundantly in mature stages. One clone in Michigan, measuring about 5 × 8 feet, contained more than 50 mature aerial stems. On a southern Wisconsin hillside collecting 25 plants made no visible reduction in the apparent abundance.

The following table summarizes the distinctions between *Uvularia perfoliata* and *U. grandiflora.* Because of the high degree of intermediacy along the zone of overlap of the two species, it is more practical to list those characters least like those of the other species. It is intended that the assumption should hold, viz., that the perfoliate *Uvularia* least like *grandiflora* is, in nature, the best *Uvularia perfoliata,* and also the converse must be true.

A COMPARISON OF THE PERFOLIATE UVULARIAS

Uvularia perfoliata (least like *U. grandiflora*)	*Uvularia grandiflora* (least like *U. perfoliata*)
Flower	
Solitary	1–4
Perianth granular-rough within	Perianth smooth within
Stamens equal in length to style or shorter	Stamens longer than style
Anthers pointed at tip	Anthers blunt-tipped
Fruit	
Capsule acutely truncate	Capsules obtusely lobed
Leaves	
Lower surface glabrous	Lower surface strongly pubescent
3 or 4 below lowest branch	One below lowest branch
Branch-subtending leaf 65 mm. or less long	Branch-subtending leaf 85 mm. or more long
5–8 per plant	13–36 per plant
Fertile branch with one leaf	Fertile branch with many leaves
Glaucous	Deep green
Smooth, thin	Rough, thick
Oval	Mature leaves shaped like a "Dutchman's shoe"
Size	
Longest internode 100 mm. or less	Longest internode 150 mm. or more

History of the Perfoliate Uvularias

The perfoliate species of *Uvularia* are sufficiently distinct from other Liliaceae to make their botanical position clear, and, with perhaps one exception, the history of this group does not show that these plants were ever confused with those of closely allied genera. What confusion has existed lies between inter-specific, rather than inter-generic, similarities.

As indicated in the preceding section, *Uvularia perfoliata* is a Linnean species and *U. grandiflora* was established by Smith in 1804. At the same time that Smith established *U. grandiflora,* he described another species from eastern America which he named *Uvularia flava.* Described as rare, *U. flava* was similar to *U. perfoliata* but with deeper yellow flowers and perianth smooth within—floral characteristics which suggest *U. grandiflora. U. flava* was recorded from New Jersey to Virginia, well within the range of *U. perfoliata,* and on the extreme eastern boundary of the distribution of *U. grandiflora. U. flava* appears to have been a hybrid between *U. perfoliata* and *U. grandiflora* and is no longer recognized as a species.

Fig. 3. Knoxville "Collection A"

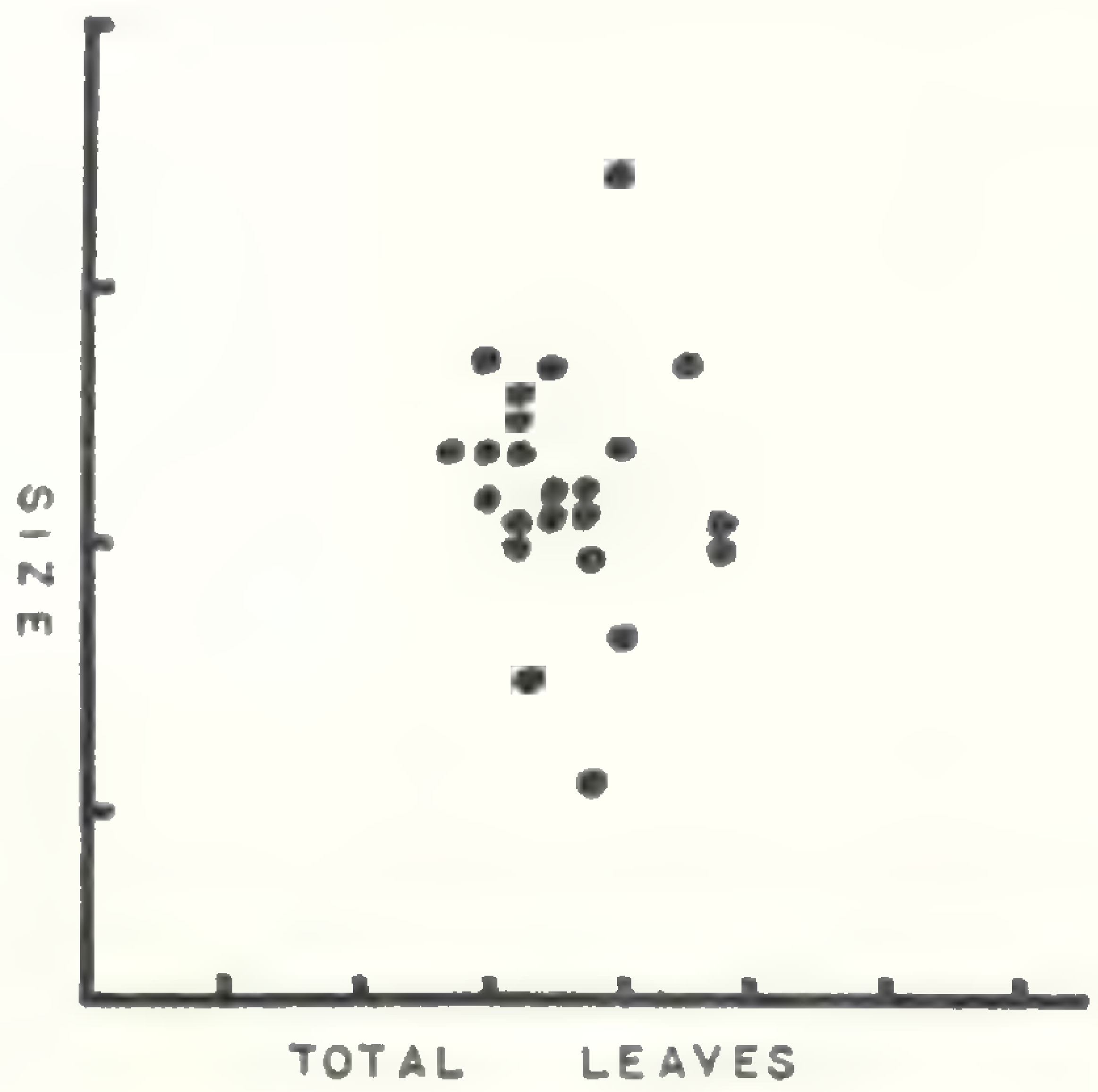


Fig. 4. Knoxville "Collection B"

These scatter diagrams show the size (length of longest internode) plotted against the total number of leaves on the plant. Note the high degree of overlap between the two collections.

Walter's collection of American plants, made in the latter half of the eighteenth century, contained a plant which he called *Anonymos (Erythronio affinis) pudica.* Walter did not collect or identify as such any plants of *Uvularia,* but from the description (Fl. Carol. 1788) his plant undoubtedly refers to a species of that genus. Michaux (Fl. Bor. Am. 1803) considered Walter's specimen to be *U. perfoliata.* In 1833 Asa Gray noted that it resembled the mountain *Uvularia, U. puberula* Michx. Unfortunately, the specimen now appears to be lost; at least it is not in the British Museum where Walter's herbarium is kept. We today have only Walter's description to show what the plant may have been. This reads, in part: "capsula turbinato-triangularis, angulis bifidis, trilocularis, trivalvis," and "foliis amplexicaulibus."

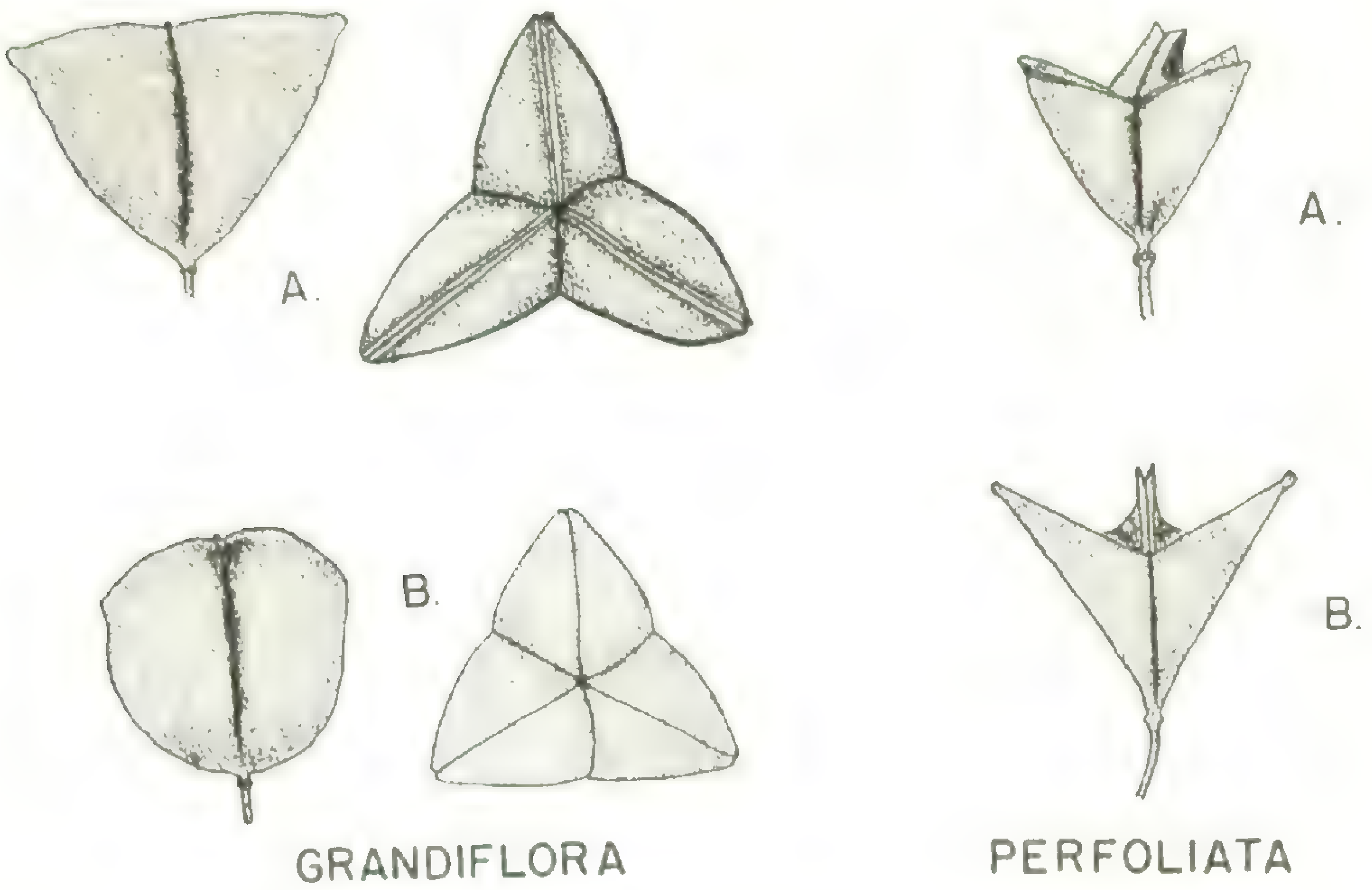


Fig. 5. Capsule types: Left—A and B, Billington; Right—A, Ridgewood; B, Monte Sano.

Fernald (Gray's Manual, 1939) uses this plant of Walter's to establish *Uvularia pudica* (= *Uvularia puberula* Michx.). *U. puberula* is a sessile-leaved plant, and the leaves are not "amplexicaul," although for a few days after the shoot of this plant appears above the ground the leaves *appear* to clasp the stem, due to their folding within the bud. Depending upon the interpretation, the capsules of either *U. puberula* or *U. perfoliata* might be considered "top-shaped." It may be that Walter's plant was a perfoliate *Uvularia,* as Michaux suggested, and not a sessile-leaved form. In any case, it appears that the name *Uvularia pudica* should be discarded and Michaux's *U. puberula* restored.

Nuttall recognized a distinction between the eastern and western populations of the perfoliate Uvularias, apparently without having read Smith's description of *U. grandiflora.* He wrote in his diary on May 14, 1810, in northwestern Pennsylvania, "There is in these swamps also abundance of a plant which I at 1st took to be *Uvularia perfoliata,* but it is much larger than I have usually seen it, the style is trifid nearly to its base; the filaments are very thick subulate & alternately longer."

The various manuals of the flora of eastern North America give the following references to perfoliate species of Uvularia:

Eaton, Amos, *Manual of Botany for North America.* 1833. Eaton notes that *Uvularia flava* equals *Anonymos pudica* Wr., and asks, "Is this distinct from the preceding [*perfoliata*]?"

Wood, Alphonso, *Flora and Class-Book.* 1846. Two species recognized, *grandiflora* and *perfoliata.* Wood notes that *flava* equals *perfoliata.*

Gray, Asa, *Manual of Botany.* 1857. Two species, *grandiflora* and *perfoliata.*

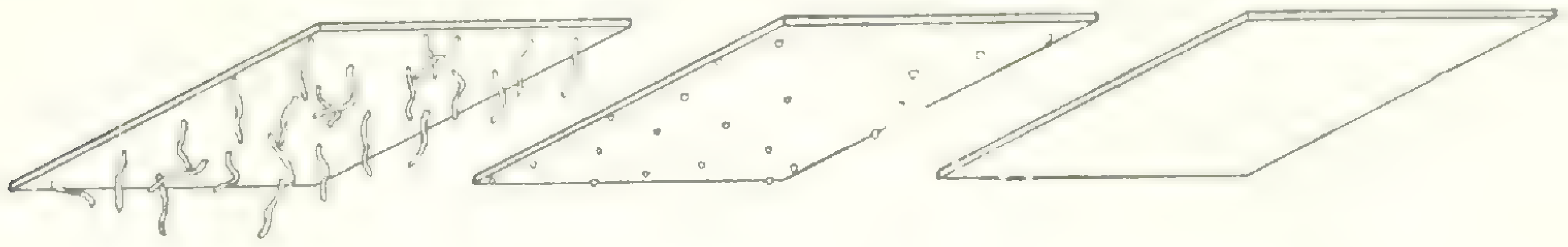


Fig. 6. Vesture types.

Gray, Asa, *Manual of Botany.* 1868. As above, with *flava* added as a distinct species.

Gray, Asa, *Manual of Botany.* 1887. The species name *flava* is dropped and never reappears in our floras.

The variation within the perfoliate Uvularias led Anderson and Whitaker to look for gross genetic differences in the chromosomes of the two species. They found (1934) that the chromosomes were so similar that the variation could not be ascribed to any gross genetic differences. In a short note, Anderson and Hubricht (1943) pointed out that the difference in leaf texture between *U. perfoliata* and *U. grandiflora* could be attributed to cellular differences in the epidermis.

From this brief history of the genus it may be seen that the problems in identification of the perfoliate Uvularias are *U. flava* and Walter's *Anonymos pudica. U. flava* may be attributed to hybridization and *Anonymos pudica* may belong with the perfoliate Uvularias rather than with Michaux's *U. puberula.* The body of this paper, then, will deal solely with the observed variations between *U. perfoliata* and *U. grandiflora,* and an interpretation of these varieties.

Analysis of Variation in the Perfoliate Uvularias

During the course of this investigation, thirty-four collections of population samples from seventeen states and one Canadian province were examined and measured. These mostly represented small collections of one to twelve specimens from any single locality. In fourteen cases, more than a dozen specimens from one locality were available. The data for each collection were transferred to a pictorialized scatter diagram to show the extent of the variation in that population. For example, in Monroe County, New York, four collections were made, three of which contained from six to twelve specimens, the fourth, thirty-five. In each the variation was measured and treated statistically, but only in the fourth collection (Oakwood Park) were the data placed in a pictorialized scatter diagram. As a result, the diagrams reproduced in this paper represent only a portion of the specimens examined and measured, but because they picture those populations from which the largest number of plants was taken, they are perhaps most valuable for determining the extent of variation in the perfoliate species of *Uvularia.*

The Pictorialized Scatter Diagram.—This technique was developed by Anderson and his students (see Anderson, 1948; Hall, 1952; Sauer, 1951) in their studies

on variation. It has an advantage over conventional scatter diagrams or graphs in that more than two characters (in this case five) may be plotted on a given set of coordinates. For diagrams in this paper, the length of the longest internode (a measure of the plant's height) is plotted on the ordinate, and the leaf index (ratio of leaf width to length; shape) on the abscissa. For a given specimen, a dot corresponding to the length of its longest internode plotted against its leaf index is placed on the chart, as in conventional scatter diagrams. From this dot, rays emanate in various positions and of varying lengths to denote other character measurements. Figure 2B illustrates this construction as applied to *U. grandiflora.* There are three rays. The center one, which stands straight up, represents the number of fruits on the plant. Where there is only 1 fruit, the ray is absent; where there are 2–4, the ray is drawn full length. The ray angling out to the left of the central one denotes the total number of leaves on the plant. Where there are 9 or less leaves, this ray is absent; where there are 10–12, the ray is very short; 13–15 leaves brings the ray out to half-length, and 16–36 leaves are marked by a full-length ray. The third ray, angling off to the right of the central arm, denotes pubescence on the lower leaf surface. An absence of this ray indicates no hairs; intermediate pubescence is shown by a line of half length; and full pubescence is shown by a full-length ray.

Charts 1 and 2 were made from herbarium specimens in the Missouri Botanical Garden. Chart 1 shows *Uvularia perfoliata,* and chart 2, *U. grandiflora.* The herbarium contains more than 200 specimens of perfoliate species of *Uvularia,* but most of these could not be measured either because they were flowering and therefore not fully grown, or they were fragmentary, or they were seedlings. All measurable plants were placed on the charts.

Uvularia perfoliata falls largely in the lower left-hand corner, and consists of dots with no arms or very short arms. The three aberrant examples with one or more long arms in chart 1 are special cases. They are all located in the southern part of the range (southern Virginia, Georgia, and Alabama) where variation in this species tends to be greater, as will be shown below. *Uvularia grandiflora,* on the other hand, tends to occur in the upper right-hand corner of the chart, and the dots are generally long-rayed.

These charts, then, reveal what is already well-known, that is, that *Uvularia perfoliata* is in general a small plant, has few leaves which are wide with respect to their length, a single fruit, and no pubescence. *Uvularia grandiflora* is larger, has many leaves which are narrower with respect to their length, more than one fruit, and is pubescent on the lower surface of the leaf. The distinctions are usually clear, indicating that the two are "good" species.

Preliminary examination of the perfoliate Uvularias, however, showed that a few populations were so intermediate that their identification was made only with difficulty, and when made it might still be open to some question. Shifting measured characters from the ordinate to the abscissa to the rays of the dots, as

well as using other characters than the five finally adopted, were tried before the final form of the charts was decided upon. This final form is an attempt to stress significant differences, in order to separate the species as far as possible, both in their position on the chart and in the number and length of the rays on the dots. As an example of this, when a collection of *U. perfoliata* and of *U. grandiflora* from two different locations near Knoxville, Tenn. were first examined, their similarity, except for pubescence, was most marked. One experiment in chart construction plotted the length of the longest internode on the ordinate against the total number of leaves on the abscissa. So plotted, the charts of each population almost exactly coincided spatially (figs. 3, 4). In the final chart form adopted, there is greater separation (charts 8, 9).

Keeping in mind the intermediacy of some collections, plants whose position on the chart fell in the lower left-hand corner and which consisted of dots with few or no rays, were considered as being less like *grandiflora* rather than more like *perfoliata*. In practice, these mean much the same thing, but in designating specimens as "less like *grandiflora*" or "less like *perfoliata*," depending on whether they fell in the lower left corner and had no rays or in the upper right corner and had long rays, we avoid the danger of setting up arbitrary standards for a species which might conceivably be at variance with the standards set up by the original describer for his type specimen. A "type" may, after all, not be "typical" of the species, yet taxonomically we cannot ignore the standards established by it on this account alone. Therefore, in analyzing the charts, we shall start with those populations least like *grandiflora* and conclude with those least like *perfoliata*.

Ridgewood, N. J. (Chart 3).—This locality is about the center of the range of *U. perfoliata*. The plants collected had invaded a rock garden in an essentially little disturbed residential area which was once a beech woods. They were not planted there, and the owner was ignorant of their presence. It might be observed that they were found in the course of a collecting trip which eventually covered over 4,000 miles, and, oddly enough, they were less than 30 feet from the kitchen door of the home of the writer's parents, a pleasant surprise to him on the halfway spot in an often discouraging trip.

All but three plants from this population were small, had 9 or less oval leaves, a single fruit, and no pubescence. The population was, in fact, less like *U. grandiflora* than any other charted. Three plants had 10 leaves, exhibiting to a very slight degree the leafiness characteristic of *grandiflora*. One plant had 2 fruits—quite unusual for *perfoliata*. In the sense that they were least like *U. grandiflora*, the Ridgewood population was the "best" *U. perfoliata* obtained in the mass collections. There is no indication that the variation is due to anything other than environment and normal heredity.

Hawley, Pa. (Chart 4).—Like the Ridgewood population, less than 100 miles away, this eastern Pennsylvania collection is in the middle of the range of *U. perfoliata*. The forest in which they were found contained areas of white oak predominance and areas of red oak predominance. The plants were found only in

the white-oak areas. There were about half a dozen sterile plants and seedlings for every fruiting plant, unlike Ridgewood where 16 of 23 plants were in fruit. The population is more variable than the preceding one with respect to leaf shape and height, but only one specimen had more than 9 leaves (it had 11) and none had more than one fruit.

In the same forest at the same time, but some distance from the previous population, in a ravine and near a creek, *Uvularia sessilifolia* was collected. The plants of *U. perfoliata* from Hawley do not show any indication of ever having formed hybrids with that species. There is some evidence that a *U. grandiflora* × *U. sessilifolia* cross has been successful in nature (see Red Lake, Minnesota), and that a *perfoliata* × *grandiflora* × *puberula* cross (the latter a sessile-leaved *Uvularia*) has occurred in Alabama (see below). It is, therefore, noteworthy that a *Uvularia* cross apparently did not occur at Hawley where two species occur together.

The high incidence of sterile (*i.e.*, non-flowering) plants in proportion to the fruiting ones was not uncommon in the collections of *perfoliata* made during this study. Plants of *U. perfoliata* were usually found spread out over a rather wide area, and only a small percentage of them were fruiting. *U. grandiflora,* on the other hand, was usually growing in tight colonies, with nearly all the plants fruiting (see Billington Woods, Mich.).

Dyestone Creek, Va. (Chart 5).—These plants were collected along the base of Smith Mountain, Pittsylvania County, on the southern border of Virginia. They are larger plants than those preceding. Nine plants (25 per cent) have more than 9 leaves; six plants (17 per cent) have the longest internode more than 100 mm. long; and one plant has 13 leaves and 3 fruits. The plant with 3 fruits and 13 leaves looks very much like a *U. grandiflora* except for its lack of pubescence.

Mountain Lake, Va. (Chart 6).—This population was located in Giles County, about 100 miles west of the Dyestone Creek population, on the grounds of the University of Virginia Mountain Lake Biological Station. An elevation of about 4000 feet makes the climate more like that in the more northern areas of *U. perfoliata* distribution, although the summer day length is, naturally, somewhat shorter. The collection was made east of the camp site. *U. perfoliata* was growing interspersed with *U. puberula.* For *U. perfoliata,* these were unusually tall plants, eight plants (61 per cent) being found with the longest internode more than 100 mm. Six plants (46 per cent) had 10 or more leaves.

Oakwood Park, N. Y. (Chart 7).—Located in Monroe County, on the east side of Irondequoit Bay, north of Rochester, Oakwood Park (apparently the name of a real-estate development) is near the western boundary of the range of *U. perfoliata.* Although the plants found here are small, like most of that species, the leaves are narrower than usual with respect to their length. Nineteen plants (54 per cent) exhibit a curious intermediate pubescence on the lower surface of the leaves (fig. 6B). Eight plants (23 per cent) have 10–12 leaves. The same intermediate

pubescence is found in two smaller *U. perfoliata* populations collected in Rochester. In the southwest portion of Monroe County a population containing both *U. perfoliata* and *U. grandiflora* was collected. *U. grandiflora* is reputed to grow around the shores of Irondequoit Bay, although none was found during a brief visit in 1951.

In many respects the Oakwood Park collection represents a high degree of intermediacy between *U. perfoliata* and *U. grandiflora*. This point is elaborated in the discussion following the presentation of charted data.

Knoxville, Tenn., Collection "A" (Chart 8).—A population was collected from the University of Tennessee farm woodlot about one mile south of the University campus, by R. E. Shanks. He described the situation as an open canopy with a heavy ground cover dominated by *Rhus*, *Laportea*, and *Galium*. This population will be discussed in conjunction with the following one.

Knoxville, Tenn., Collection "B" (Chart 9).—This sample was collected on the same day as the preceding one by Dr. Shanks from a wooded slope on the University farm. It was found under a heavy canopy of mixed deciduous trees, in a ground cover rich with *Trillium*, *Hepatica*, *Disporum*, *Polygonatum*, *Smilacina*, and *Viola*.

These populations represent our best mass-collection data on the perplexing problem of intermediacy. From a casual inspection, the plants from both collections appear to be *Uvularia grandiflora*. Closer inspection reveals that collection "A" consists of plants with leaves glabrous underneath. Still closer inspection shows that one plant of collection "A" possesses a single leaf with full-length hairs near the base on the underside. When this particular sample is under the binocular dissection microscope, the visible field is in no way different from that characteristic of *U. grandiflora*, although the rest of the leaves when viewed under the microscope are characteristic of *U. perfoliata*.

The label for collection "A" states that it is a population of *U. perfoliata*, while that for collection "B" states that it is a population of *U. grandiflora*. There is no question but that collection "B" consists of essentially *U. grandiflora* plants. However, when Chart 9 is compared with the charts which follow, the Knoxville *U. grandiflora* plants are found to be rather uniformly smaller than is typical for that species and are generally less heavily fruited. In addition, only six plants (19 per cent) have as many as 16 leaves, and five plants (16 per cent), have 12 or less. In short, the Knoxville *U. grandiflora* plants plot out on the chart as a group somewhat closer to typical *U. perfoliata* than any other group of *U. grandiflora*.

Collection "A" is a more questionable population. These plants exhibit characteristics of both species. As a group, they lean perhaps more toward *U. perfoliata* than toward *U. grandiflora*. The rather large size of the plants, and the leaf shape as reflected in the leaf indices, is more like *grandiflora* than *perfoliata*. Similarly, eight plants (40 per cent) have 13 or more leaves, and only six plants (30 per cent) have 9 or less leaves. The population is, therefore, leafier than is usual in

U. perfoliata. On the other hand, with the exception noted, the plants have the typical glabrosity of *U. perfoliata.* In another characteristic, not plotted on the chart, twenty plants (100 per cent) had 2 or more leaves below the primary branch, and seven of these (35 per cent) had 3 or more. This leafiness below the primary branch is characteristic of *U. perfoliata.* Collection "B" exhibited more of this characteristic than is usual in *U. grandiflora,* but not to the degree of collection "A."

Both Knoxville collections, then, represent intermediate plants. In collection "B" the taxonomic classification is not difficult; collection "A" is more of a problem. This area is used by classes of the University of Tennessee for ecological studies. It is a valley, rather wet at the bottom, with sloping hills delimiting it. Collection "A" was made on the bottom lands and collection "B" on the hillside, each in a distinct environment. Ordinarily one might expect to find *U. grandiflora* populations in moister locations than those of *U. perfoliata,* but the *grandiflora* populations were from the hillside of the campus and the *perfoliata* collection in the moister bottom area.

Debbink, Oconomowoc, Wisc. (Chart 10).—Near the shore of Lac La Belle, Oconomowoc, *Uvularia* was growing under an open canopy of *Tilia, Ulmus, Acer,* and among *Smilacina, Podophyllum, Pteris,* and *Equisetum.* Although clearly *U. grandiflora,* plants in this collection are smaller than usual for this species, and the leaf shape is quite variable. Only three plants (12 per cent) have more than one fruit. Ten plants (40 per cent) have less than 16 leaves, although one plant has 27. The leaf color of the fresh specimens was quite variable, ranging from deeply bluish-green, through dark green to yellowish-green.

La Barque Creek, Mo. (Chart 11).—Found in mixed woods at the base of a sandstone bluff in the La Barque Creek area south of Eureka, Missouri, this collection consists of moderately large plants with narrower leaves than usual for *U. grandiflora.* Notable in this population is the complete absence of plants with more than one fruit. *U. sessilifolia,* like *U. perfoliata,* is typically a single-fruited plant. It is found in Missouri, although more frequently north of the Missouri River than south of it.

Butts, Mo. (Chart 12).—Another small collection like the preceding was gathered from low woods near Courtois Creek. It is a little more typical of *U. grandiflora* than the La Barque Creek population. On only one plant is the longest internode less than 150 mm. Six plants (46 per cent) have 16 or more leaves; all plants have 14 or more leaves.

Red Lake, Minn. (Chart 13).—These plants from northern Minnesota are far removed from any juxtaposition with *U. perfoliata,* and, on the chart, they tend to congregate in the upper right hand corner, as should be expected for *U. grandiflora.* However, the fact that twenty-four plants in the population (96 per cent) lack three full-length rays on the dots used to plot them indicates that in some manner they fall short of being "good grandifloras." This point is discussed following the description of the charted data.

Clarksville, Mo. (Chart 14).—The Clarksville population was collected on the upper slopes of one of the characteristic glacial knobs of southern Pike County. The plants were growing under a heavy canopy of mixed deciduous trees, with *Bidens, Hystrix, Smilacina,* and *Polygonatum.* Although the leaf indices of this population are quite low, there are only three plants (11 per cent) whose longest internode is greater than 200 mm., and only two plants (8 per cent) which, on the basis of all five characters, are "good grandifloras." These two plants are in the upper right portion of the chart.

Coxsackie, N. Y. (Chart 15).—Coxsackie is in Greene County, on the Hudson River about 22 miles south of Albany. It is therefore well within the range of *U. perfoliata.* Six plants (31 per cent) are really "good grandifloras"; that is, they are tall, have a low leaf index and a complete set of full-length rays on the chart. These six plants are, in general, in the upper right portion of the chart. The smallest plants charted tend to have higher leaf indices and incomplete ray systems; in other words, the plants in the lower portion of the chart tend to be less *grandiflora*-like than the others.

Missouri (Chart 16).—This chart depicts a synthetic population. It was constructed from material in the Missouri Botanical Garden Herbarium which had been collected in Missouri. As a rule, there is only one plant from each county. Most of the plants were not mature and fruiting; the 35 plants which were measurable are included on the chart.

These plants plot out rather well for *U. grandiflora.* Fourteen plants (40 per cent) have complete sets of rays on the dots used to plot them. The "average plant" has the longest internode, 191.4 mm., a leaf index of .372, 16½ leaves, and 1½ fruits, and is fully pubescent. With the addition of half a fruit, this rather grotesque "average plant" would make an excellent *U. grandiflora.*

This general Missouri collection averages more like *grandiflora* than the individual Missouri collections. The explanation may lie in the fact that plant collectors usually strive to collect the best specimens for herbarium material, whereas a mass collection aims for a cross-section of the population.

Billington Woods, Institute Grounds, Bloomfield Hills, Mich. (Chart 17).—This *Uvularia* population, which appears to be a single clone, covered an area of about 5 × 8 feet, and contained well over fifty fruiting stems, crowded too closely together for exact counting. The plants were growing in a moderately open place in deep, moist woods. The adjacent trees were *Ulmus fulva, Carya tomentosa, C. ovata,* and *Cercis canadensis. Osmorhiza* grew around the edge of the clone.

This population was the least *perfoliata*-like of the mass collection material. There was a high percentage of secondary and even tertiary branching. Thirteen plants (72 per cent) had more than one fruit; the average was 2.5, as many plants had 3 fruits, and a few had 4. Other averages, which reveal the *grandiflora* characteristics of the population, are as follows: length of longest internode, 200.5 mm.; leaf index, .298; total leaves, 17; pubescence, complete in all specimens.

UNCHARTED COLLECTIONS

Some smaller collections, not charted, are nevertheless noteworthy, and are listed below:

Natchitoches, La.—In 1935 Anderson noted the existence of *U. perfoliata* in a woods along Grand Ecore Road, about two miles west of Natchitoches. Natchitoches is an extension of the previously known range of *U. perfoliata* by about 400 miles. These woods range from dry to wet enough for *Taxodium* with well-developed "knees." Occasional trees bearing *Tillandsia usneoides* provide an environment contrasting strongly with that of *U. perfoliata* in New England.

Five specimens, including Anderson's and several from the herbarium of the Northwest Louisiana State Teachers College, are available for study. All have at least three leaves below the single branch. All are small plants, with few leaves. Four are too early in the fruiting stage to get much of a picture of capsule shape, or more than a general picture of the ultimate measurements. This general picture suggests, however, that these plants are remarkably "good perfoliatas." The nearest plants of *Uvularia grandiflora* are some 250 miles to the north, in central Arkansas.[2]

Monte Sano, Ala.—One plant and several fragments from the herbarium of the New York State Museum came from rich woods, over limestone, near the summit of Monte Sano in Madison County. The size and shape of the leaf are as in *U. grandiflora.* All the leaves of the pressed specimens are so thin and translucent that newspaper sub-heads can be read clearly through them. Most of the leaves are completely glabrous, those which are not glabrous are very sparsely pubescent; where *U. grandiflora* will have well over 10 hairs per sq. mm., these plants have 1 hair to about every 5 sq. mm. The pubescent specimen in Knoxville "A" was completely pubescent, and the Oakwood Park specimens with intermediate pubescence had these emergencies with the same relative density as typical *U. grandiflora.* One of the fruiting specimens from Monte Sano contained a detached flower, which may or may not have belonged to it. The inner surface of the perianth segments of this flower was smooth, as in *U. grandiflora,* but there were about three places on each segment where rudimentary papillae could clearly be seen. The population sample is too small for the formulation of any definite conclusions.

If it be possible, an even more perplexing specimen—a single sheet in the Missouri Botanical Garden Herbarium (#1267594)—from Scottsboro, Alabama—possesses characters of *U. perfoliata, U. grandiflora,* and *U. puberula.* It has leaves slightly pubescent on the dorsal surface, an extreme *perfoliata* fruit, and angles of the stem are pubescent. Furthermore, although perfoliate, the form of the plant is more like *puberula* than either of the perfoliate species.

From these rather meager data, it appears as though the perfoliate Uvularias from northern Alabama are at least as variable as the Rochester or the Knoxville populations.

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[2] A collecting trip to Natchitoches in 1951 failed to augment these with mass-collection data.

An Interpretation of the Variation in the Perfoliate Uvularias

The concept of introgressive hybridization was developed by Anderson (Anderson and Hubricht, 1938; Anderson, 1949, 1950). Introgressive hybridization, or more simply, introgression, may be defined as the inherited variation in a species which results from back-crossing an original hybrid with one parent until only a small amount of the germ plasm of the other parent remains. Frequently, the effect of so small an amount of foreign germ plasm is not immediately apparent in the mongrel offspring, and must be detected by statistical or experimental means. *Uvularia* is a perennial plant, and under the best conditions each generation will take two years to grow to flowering size. In nature, some plants—particularly those of *U. perfoliata*—apparently take even longer. Experimental hybridizations and back-crosses would have involved a prohibitive amount of time. Further, since the primary question in this investigation was whether introgression is occurring in natural populations, we adopted the statistical treatment. The charts in this paper are designed to provide critical evidence for or against the presence of extensive introgression. Theoretically, continual back-crossing to the parental species would at length produce offspring in which the effect of the foreign germ plasm was so dilute that it could be detected only by the most elaborate genetic tests, if at all.

In order to study introgression, it is valuable first to become familiar with plants in which there is reason to believe it is not a factor. This led, in the present project, to the quest for "good perfoliatas" and "good grandifloras." A study of the presumably "good" specimens led to temporary criteria for these species, such as glabrousness *vs.* pubescence, relative leafiness, relative size, branching pattern, leaf shapes, etc. With the acceptance of temporary criteria, preliminary plots of the "good" populations may be drawn up. It is important that the characters used for the ordinate and the abscissa be such that for one "good" species the values will fall in one corner of the diagram, while for the other species they fall in the opposite corner. An intimate relationship between the two species would be shown by the fact that intermediates fall at some point between the two corners reserved for the "good" species, and none in the unassigned corners of the chart. In this project, following the traditional orientation of the pictorialized scatter diagram, our charts reserve the lower left corner area for one species, *U. perfoliata,* and the upper right corner for *U. grandiflora.*

The rays on the dots are so planned that one "good" species (in this case *U. perfoliata*) should be ray-less, while the other will have a complete set of full-length rays. If the variation depicted by the rays is related, we must expect that, as the dots progress from the lower left area of the chart into the upper right, the frequency and length of the rays will tend to increase correspondingly. And if that condition appears on the chart, we cannot escape the conclusion that the condition is caused by an intimate relationship between the two species.

If introgression is a factor in the populations reproduced on the charts, what evidence for this fact appears on them? The answer reveals one of the peculiar

advantages of the pictorialized scatter diagram over other methods of data presentation for the analysis of variation. On the charts, where introgression is a factor, there is a strong tendency for the sum of the measured characters to vary together. The total variation is more cohesive than the variation of the single characters making up the total. The following examples illustrate this fact.

In a population which is varying due to some environmental factor, as of a plant which grows large and lush along a stream bank and becomes gradually smaller, less branched, etc., as it grows up a slope, the variation would be something like that in fig. 7. The dots would fall on a straight line, and the rays would all increase proportionately as the dots progressed from the lower left area to the upper right.

In introgressive populations, on the other hand (fig. 8), the position of the dots forms a spindle-shaped figure of various proportions. The only areas on the chart where no dots will fall are the two unassigned corners. As the dots progress from species "A" to species "B" the sum of the rays becomes, on the average, increasingly greater, although the progressive increase of any individual ray may appear to be a random one. Note that for any given value midway on the ordinate, the values may fall along several places on the abscissa. Further, the equally variable picture presented by the rays indicates that the mongrel examples of the population express a wide recombination of characters, just as has been found in experimental crosses and back-crosses between species and races. The tendency for any one character to correlate with the sum of the other characters is therefore greater than the tendency of a single character to correlate with that of any other single character; that is, introgression (as opposed to an environmental relationship, for example) shows recombination of characters expressed as a total tendency and not as a simultaneous correlated progression of the component characters.

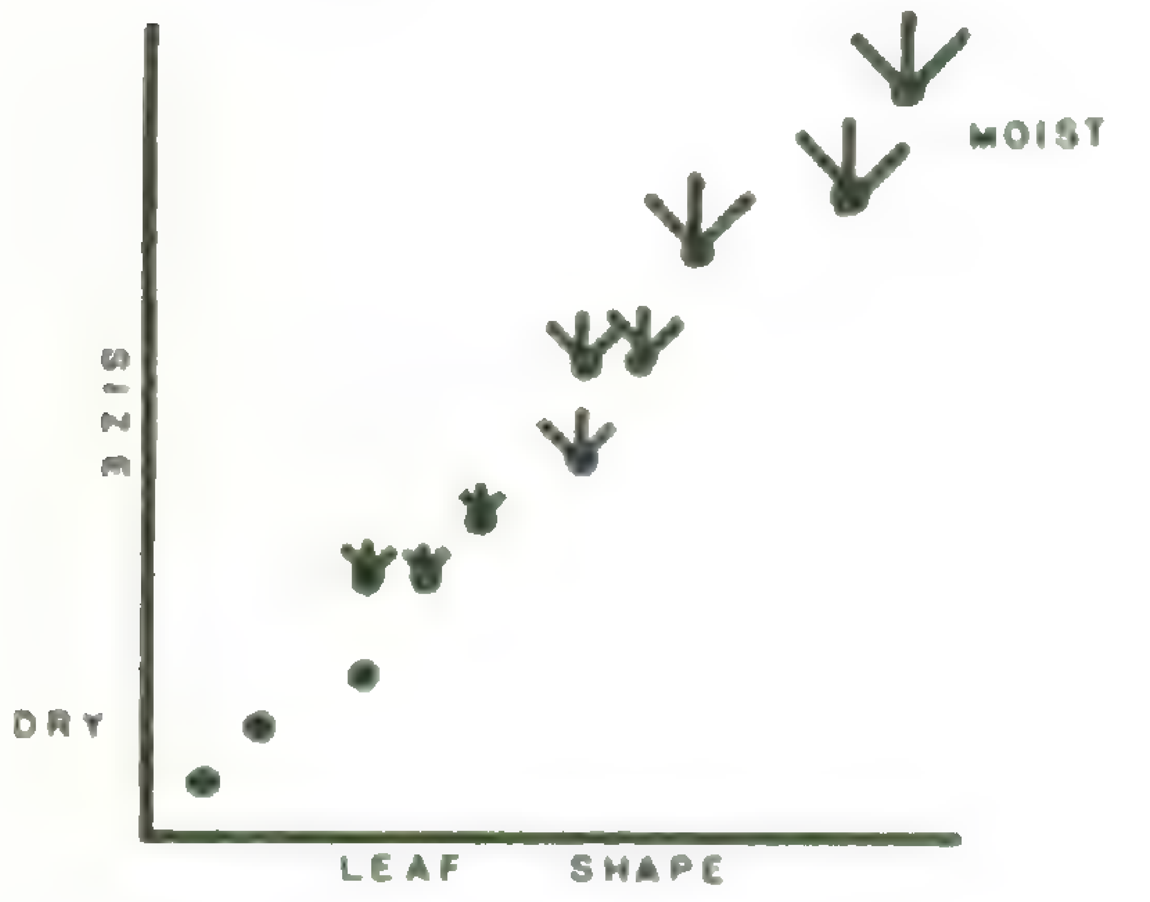

Fig. 7. A hypothetical species in which variation is due to environment. As the environment changes from moist to dry, the plant becomes increasingly small in each character. No outside genetic influence is working on the variation pattern.

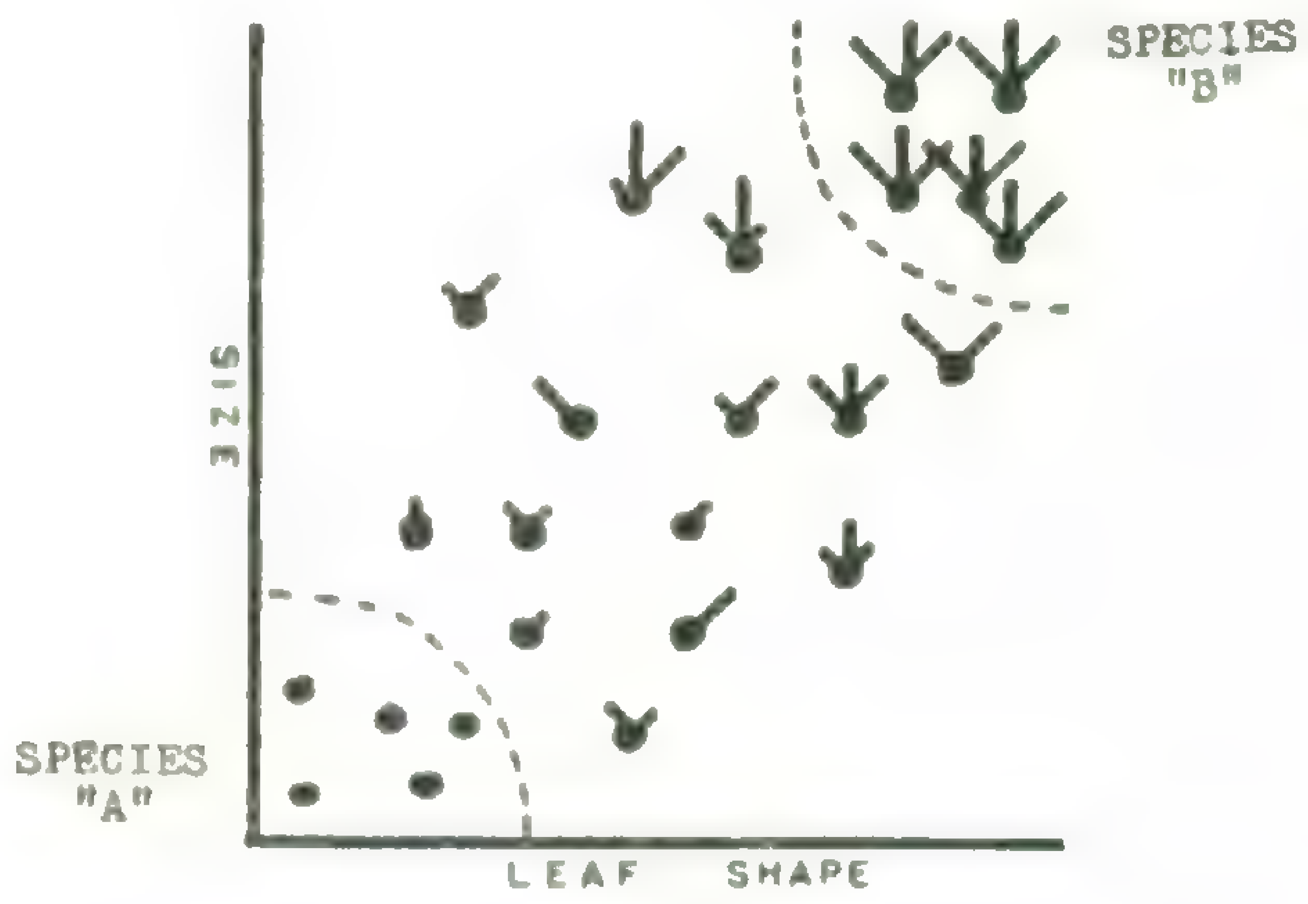

Fig. 8. Species in which introgression is causing the variation. The total ray pattern becomes greater toward the upper right-hand corner, expressing the fact that the total variation is more directional than that of any of the component characters.

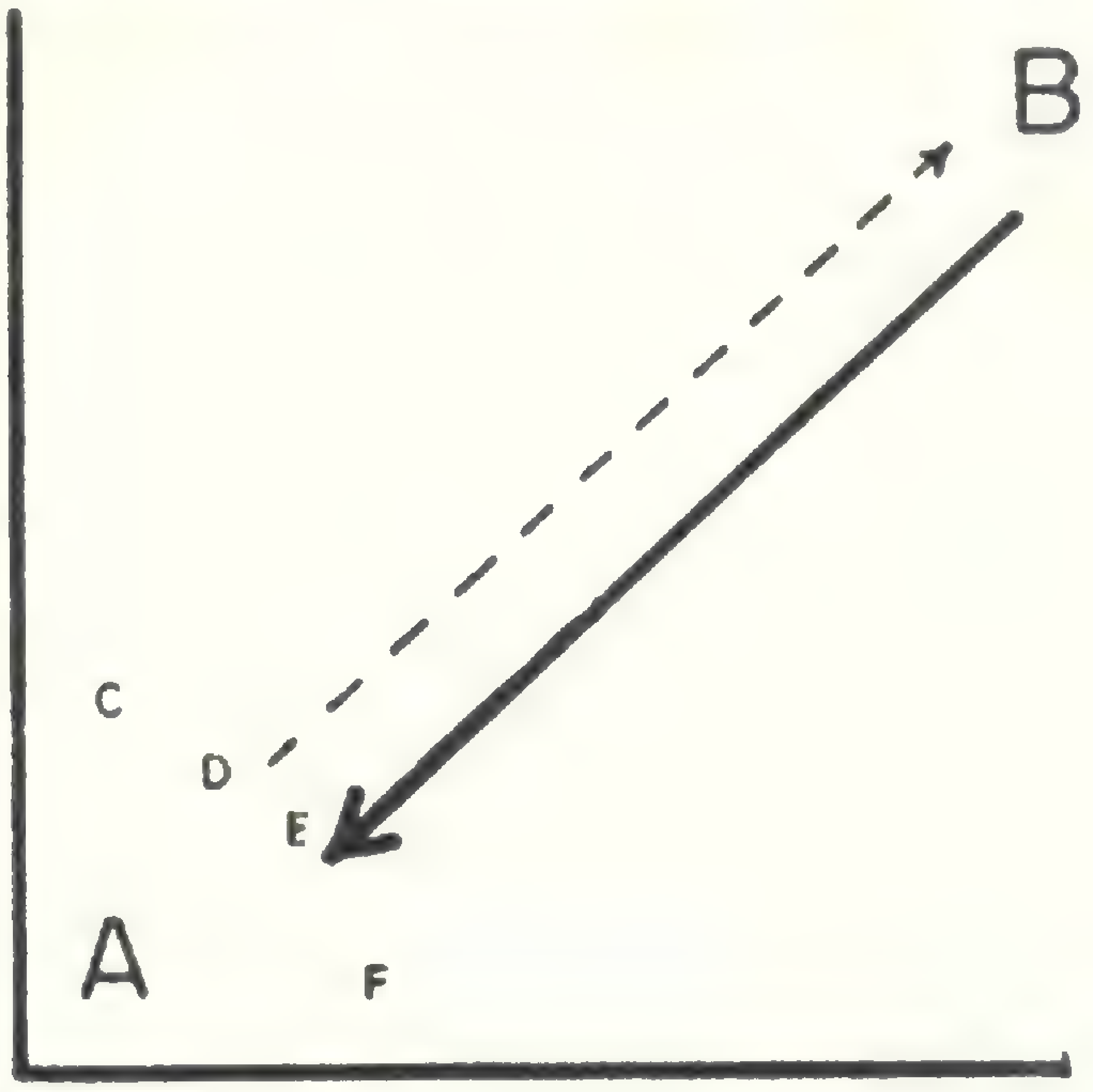

Fig. 9. See explanation below.

The ease of analyzing introgression depends upon the possible number of taxons (taxonomic entities) involved. If there are only two, the problem is simple; with three or more, it is usually very complex.

In the genus *Uvularia* there are six taxa (*U. perfoliata, U. grandiflora, U. sessilifolia, U. puberula, U. puberula nitida,* and *U. floridana*). None of these exists separated by any great distance from any one of the other perfoliate species. In some parts of the range, four taxa occur in the same geographical area. This fact raises the problem of detecting introgression between *perfoliata* and *grandiflora* without obtaining data obscured by factors originating within the taxa with which we are not presently concerned (see fig. 9, above). *Uvularia grandiflora* is markedly distinct from all the other species of *Uvularia* in a great many characters—a heavy branching pattern, multiple fruits, numerous leaves, etc. If we assign *U. grandiflora* to the upper right area of the chart, and *U. perfoliata* to the lower left area, the other four taxa might fall in a way suggested by the letters CDEF. This general picture is what we find in the present project. Actually, the four other taxa represented by CDEF, while relatively close to *U. perfoliata,* would more properly be charted in four other dimensions, although remaining in a projection of the lower left area of this chart.

In a case of this kind, we can secure valid introgression data only in the direction indicated by the solid arrow, that is, introgression of *grandiflora* into *perfoliata.* Introgression data from *perfoliata* to *grandiflora,* in the direction of the dashed arrow, would be obscured by the presence of the elements CDEF, which would come from the same direction. Because of the morphological resemblance between the various species of *Uvularia* in eastern North America, introgression of *grandiflora* into *perfoliata* is easy to detect and even, within certain limits, to

measure. Introgression of *perfoliata* into *grandiflora*, on the other hand, is so obscured by the presence of other species similar to *perfoliata* that we have no critical data for or against it.

In spite of its shortcomings, the type of statistical treatment used in this paper is superior to the standard methods of determining population averages using means, extremes, and spread, and calculating correlations from those data. The following table uses population means to describe the average plants of the fourteen field collections and three herbarium collections used in our charts. We learn little from this table except that *U. grandiflora* is generally larger than *U. perfoliata*, has a lower leaf index, more leaves, more fruit, and is pubescent as opposed to glabrous. This we already knew. If we calculated standard deviations we would discover that some populations varied more than others, and that these populations were from the area corresponding to the western boundary of *U. perfoliata*. The early statistical work in this project was done in this standard manner.

While the standard statistical procedures can and do tell us that the populations are different, and that some vary more than others, they do not tell us from whence this variation originated. The pictorialized scatter diagrams do give us this picture, subject to the restrictions outlined above.

Once the temporary criteria for "good" species are drawn up, preliminary charts may be constructed which enable us to refine our criteria to the point where the pattern of variation, if any, becomes clear. When this pattern is established, it becomes less difficult to select those characters for study which seem to express the variation pattern most clearly and to eliminate the variation which is not connected to the problem. The idea is not to construct a chart in which variation is stressed, but rather one which will express only the most essential differences between populations. If the preliminary survey of the problem indicates that introgression is not a factor in the species variation, there is no use to refine data, for no amount of data-juggling will result in a pattern which implies that introgression is a factor in the species variation.

Pictorialized scatter diagrams are just as good for demonstrating that introgression has not taken place as for showing that it has. The method was originally worked out for recording variation in fields of maize (Anderson, 1946). Begun as a purely mnemonic device, it demonstrated the importance of crosses between races of maize, and this led to its use in analyzing crosses between species of flowering plants. It is a general method of demonstrating the over-all picture in variation patterns too complex for unaided analysis. It is as useful for demonstrating the absence of character association as for its presence.

Collection	Length longest internode (mm.)	Leaf index	Total leaves	Number of fruits	Pubescence
Missouri Bot. Gard. *U. perfoliata*	95.4	.498	10.1	1.28	Absent
Missouri Bot. Gard. *U. grandiflora*	183.7	.388	15.7	1.47	Complete
Ridgewood	85.4	.506	8.9	1.06	Absent
Hawley	97.1	.461	7.4	1.00	Absent
Dyestone Creek	114.2	.560	8.2	1.00	Absent
Mountain Lake	107.1	.508	9.0	1.00	Absent
Oakwood Park	90.6	.443	8.3	1.00	Intermediate
Knoxville "A"	145.4	.431	12.4	1.05	Partial
Knoxville "B"	160.0	.346	14.2	1.06	Complete
Debbink	159.1	.352	16.3	1.12	Complete
La Barque Creek	172.0	.284	15.8	1.00	Complete
Butts	174.0	.342	15.0	1.15	Complete
Red Lake	184.1	.338	14.9	1.04	Complete
Clarksville	173.0	.306	14.5	1.08	Complete
Coxsackie	184.0	.354	15.6	1.37	Complete
Missouri Bot. Gard. "Missouri"	191.4	.372	16.5	1.50	Complete
Billington Woods	200.5	.298	16.9	2.46	Complete

Collections Giving Evidence for Charted Data

Ridgewood, N. J. (Chart 3).—Thirteen of the sixteen plants plot out as "good" *perfoliata*. There is some variation in the population, three plants having more than 9 leaves, and one with 2 fruits. While these characters tend to suggest *U. grandiflora*, there is no clear evidence that introgression has been a factor in the Ridgewood population. A 2-fruited *U. perfoliata* is atypical, but not outside the realm of normal variation for an occasional plant. If the 2-fruited plant were in an extreme position toward the *grandiflora* corner of the chart it would come under suspicion, but this is not the case.

Hawley, Pa. (Chart 4).—This is another "good" *perfoliata* population, the variation in which is mostly in the direction of larger plants with somewhat narrower leaves than is typical of *U. perfoliata*. However, since there is no concomitant increase in the ray pattern to accompany this variation, we must reject introgression in this population.

Dyestone Creek, Va. (Chart 5).—The Dyestone Creek population is composed largely of "good" *perfoliata* elements, but there is evidence that there has been some influence here from *U. grandiflora*. Of the six plants appearing highest on the internode scale, five are seen to have one or more ray fragments. On the other hand, the five plants lowest on the internode scale are devoid of rays. It then follows that the variation in this population is oriented toward *U. grandiflora* rather than simply at random. Dyestone Creek is not far from the "fringe" area in which the variation in *U. perfoliata* is so marked. There is, in fact, a suggestion in this collection of the variation pattern which will appear in the "fringe" area populations.

Mountain Lake, Va. (Chart 6).—Although west of Dyestone Creek and therefore nearer the "fringe" area, the Mountain Lake population apparently has not been influenced by introgression from *U. grandiflora*. The population contains taller plants than typical for *perfoliata*, but this may be due to environment, since there are no other connected tendencies toward *grandiflora*. There are, however, some populations in the Mountain Lake area which apparently have been influenced by introgression from *U. grandiflora*. The Mountain Lake Biological Station herbarium contains some sheets of *Uvularia*, several of which preserve what we would call "problem plants." These are occasionally identified incorrectly, but frequently they may possess some key characters of both species, and even a person familiar with the plants could conceivably be led astray. The Mountain Lake area contains plants of *U. perfoliata*, *U. grandiflora*, and some intermediates, as well as two other species of *Uvularia*.

The fact that our population sample does not show introgression serves to point up the fact that, even in "fringe" areas, only occasional populations display this feature. Although most of the observed intermediate populations come from "fringe" areas, it should not be implied that all fringe-area populations are intermediate.

Oakwood Park, N. Y. (Chart 7).—This population is near the western boundary of *U. perfoliata* and therefore in the "fringe" area where the greatest variation has been noted. We now can observe that this variation is due to introgressive hybridization. While the entire population consists of rather small plants, the leaves are uniformly narrower than those in Ridgewood, for example, and the picture presented by the rays shows that the *grandiflora* elements appear generally from the direction which was assigned to that species. The dots in the lower left area of the chart are generally without rays. Those in the upper right portion are all partially rayed. This is the population in which we found the intermediate pubescence. The rays are not distributed at random on the chart, but instead follow a path from the upper right, or *U. grandiflora* position. Therefore the population is intermediate because of introgressive hybridization.

Knoxville, Tenn., Collection "A" (Chart 8).—This population is really intermediate. It is located near the center of the chart, midway between *U. perfoliata* and *U. grandiflora*. In addition, the rays are more frequent and longer in the upper right portion of the plot. The plant in the lower left has a long ray to the right, indicating pubescence. While there is no doubt that this is a *grandiflora*-type pubescence, it only appeared on a portion of a single leaf and the rest of the plant was glabrous. Had we called the plant glabrous, the dot would have appeared with only a fragment of a ray off to the left, indicating a slight leafiness.

The population, essentially *U. perfoliata*, is growing in a moist area. This is not usually true for "good perfoliatas." The fact that the plants do well in this environment may be attributed to the adaptability they have acquired as a result of the introgression from *grandiflora*.

Knoxville, Tenn., Collection "B" (Chart 9).—This is essentially a *U. grandiflora* population. The picture presented by the rays presents a generally random variation. The plants average smaller than "good" populations of *U. grandiflora* should, but there is no evidence to indicate that size is not an environmental condition, or, if the result of introgression, from which small *Uvularia* the condition came.

Debbink, Wisc. (Chart 10).—These plants, like the preceding ones, are small for *U. grandiflora*. There is a slight tendency for the rays to be longer in the upper right portion of the chart than in the lower left. However, again we have no way of determining the origin of the non-*grandiflora* element which this tendency reflects, if there is actually such an element in the population.

La Barque Creek, Mo. (Chart 11).—Although variable, the variation is at random in this charted population.

Butts, Mo. (Chart 12).—The position and totality of the rays on this chart offer a faint suggestion of introgression from some non-*grandiflora* source.

Red Lake, Minn. (Chart 13).—The variation in this population with respect to *perfoliata-grandiflora* introgression is at random. Though outside the scope of this investigation, the Red Lake collection suggests strongly an introgression from *U. sessilifolia*.[3] This is reflected in the chart by the rather amorphous variation of the plots. There is no tendency toward *U. perfoliata*, in spite of the low degree of cohesiveness. This fact tends to indicate that the design of the charts has met with the demand that it reflect the *grandiflora-perfoliata* tendency without influence from other variation factors.

Clarksville, Mo. (Chart 14).—In this collection we see again a faint suggestion of introgression from a non-*grandiflora* element. There is no indication that this element is *U. perfoliata*.

Coxsackie, N. Y. (Chart 15).—The Coxsackie collection is from an area where the two species grow near to each other. While the population as a whole is quite *grandiflora*-like, there is a strong suggestion of introgression with *U. perfoliata*. This may indeed be true, but the design of the chart is such that introgression from *U. perfoliata* into *U. grandiflora* is not provable. However, since we have striven to eliminate much of the variation from directions other than that between *perfoliata* and *grandiflora* from the chart, we can state that the Coxsackie population probably represents introgression from *perfoliata* into *grandiflora*.

Missouri (Chart 16).—This synthetic population sample from herbarium sheets in the Missouri Botanical Garden reflects the general condition found in the individual Missouri collections. As a whole, these plants represent a "good" *grandiflora*. There is a slight tendency for plants with complete ray systems to be higher and farther right on the chart than those with incomplete ones, but there is no proof that this variation is from *U. perfoliata*.

[3]This suggestion is expressed by the following facts: (1) the presence of some sessile leaves on the upper portions of occasional plants; (2) the 90° angle of the primary branch, as in *U. sessilifolia*, rather than one of about 60°, as in *U. grandiflora*; and (3) the gross appearance of the plant which is similar to that of the sessile-leaved species of *Uvularia*.

Billington Woods, Mich. (Chart 17).—This is, on the whole, an excellent population of *U. grandiflora.* Of the eighteen plants, fourteen (78 per cent) have 3 rays, and of these fourteen plants (67 per cent of the total) have complete ray systems. The four plants with only two rays appear at random on the chart.

Interpretation of the Variation in the Perfoliate Uvularias

As has previously been discussed, the only clear evidence for or against introgression in the perfoliate species of *Uvularia* is from *U. grandiflora* into *U. perfoliata.* The *grandiflora* populations are often quite variable, but we cannot prove that this is due to introgression from *perfoliata.* On the contrary, we have reason, from the charted data, to believe that in many cases this is not true. The Coxsackie *grandiflora* population appears to have been influenced by introgression from *perfoliata,* and the chart indicates that this is probable, but other non-perfoliate species might be involved.

One of the most significant facts to be gleaned from the charted data is the relative rarity of introgression as a factor in the perfoliate Uvularias. We can reason that if these species hybridized easily in nature, large numbers of hybrid populations would occur throughout the area of mutual distribution. This is not so. Generally, throughout the area of overlapping distributions, each species population is distinct. Most of our typical specimens of *U. perfoliata* come from areas where *U. grandiflora* is not far away.

Once a hybrid does occur in nature, however, the way is clear for introgression to proceed. *Uvularia* is a perennial plant. It is not necessary for it to set seed each year in order to survive. Propagation is largely vegetative. The F_1 plant, then, once it occurs, can exist without genetic change (unless by mutation) for a long period of time. Since we have reasoned that these F_1 plants must be rare, it follows that at such a time as cross-fertilization occurs again in that plant, it must be between the F_1 and one or the other parent species, most likely the one closest by; in other words, a back-cross. This back-cross will resemble the parent with which the F_1 was hybridized, except that some of the characteristics of the other species may remain. In time this back-cross generation may again hybridize with the primary parent species. The cross would logically occur thus, since we have postulated that the F_1 hybridized with the parent species most adjacent to it, and the back-cross would behave similarly. Thus a second back-cross generation is formed which contains no less than seven-eighths of the characteristics of the primary parent species and no more than one-eighth of those of the secondary parent species. Genetically, it is possible to reconstitute the original species even in the first back-cross. In nature, those back-crosses with the fewest elements of the foreign species are those most likely to survive under natural conditions (Anderson, 1948). As a result of crossing between the two species, we are most likely to find back-crosses closely resembling the original primary parent species but slightly variable in the direction of the non-recurrent parent. The results of such hybridizations and back-crosses is that a genus such as *Uvularia* could persist unchanged for long periods of time, hundreds or even thousands of years.

The question then arises: Why should this condition not be prevalent throughout the areas shared in common by the two species, rather than primarily at the edge of the range of *U. perfoliata*? Away from the "fringe" areas of the specific distributions the environment is relatively uniform, and the potential parents are occupying ecological niches for which they are suited. Occasional crosses present no particular advantage to the hybrid, or they may even present something of a disadvantage with respect to the niches for which the parents have become adapted. After a time the hybrids would tend to disappear. This may have been the case with *U. flava*, the species which Smith established at the same time that he established *U. grandiflora*. *U. flava* appeared to be essentially like *U. perfoliata*, but it possessed flower characteristics like those of *U. grandiflora*. From the descriptions it appears that *U. flava*, considered rare and found "from New Jersey to Virginia," was probably an introgressive hybrid, or perhaps even an F_1, which did not add any particular advantage to the *perfoliata* element. *U. flava* apparently disappeared gradually, for the manuals of the day reflect increasing uncertainty about it until it finally was dropped into synonymy with *U. perfoliata* and was removed entirely from the literature. We have found no records of *U. flava* collections for more than sixty years, nor do we know of any botanists who claim to have seen this form in recent years.

What then is the significance of introgression as a factor in the perfoliate species of *Uvularia*? Introgression provides a reserve of adaptability on which the plant can draw, under conditions differing from those for which the parent species have become adapted. If conditions change, or if the plant migrates away from the area in which the parent species are successful, this reserve is available, with the consequence that the introgressive hybrid is more likely to be successful. The successful form differs, albeit slightly, from the parent species. Projecting this into the future, the introgressive hybrid represents a possible step in the differentiation of another kind of plant. It is the potential ancestor of a new species, which can survive and evolve in environments where the parent species would be less likely to do so. It is free to evolve to occupy a different niche than those which its relatives occupy.

The study of introgression properly belongs in the field of micro-evolution, which sheds light on a portion of the still greater field of evolution itself.

Summary

Over most of their ranges, two species of *Uvularia, U. perfoliata* and *U. grandiflora*, are good and distinct species. There are some populations, however, which are quite variable and possess characters intermediate between the two species. These populations are most frequent along a line roughly corresponding to the western border of the distribution of *U. perfoliata*, and this species exhibits the greatest portion of the observed variation.

It was suspected that this variation was due to introgressive hybridization. To determine whether or not this were true, extensive measurements of both the good

species and the variants were taken. Introgression is generally so subtle that special methods for its detection must be employed. These methods may be either statistical or experimental. Since *Uvularia* is a perennial, and the experimental data would involve a prohibitively long investigation, the statistical method was employed. Because of the presence of other species quite similar to *U. perfoliata,* it is shown that introgression from *perfoliata* into *grandiflora* would not be readily demonstrable, although the reverse introgression *(grandiflora* into *perfoliata)* could readily be demonstrated if it does indeed occur.

The statistical data were reduced to charts designed primarily to reveal the influence of *grandiflora* on *perfoliata,* if such influence existed. The charts demonstrate introgression from *grandiflora* into *perfoliata* in some populations.

These introgressive populations were most abundant along the western border of the distribution of *U. perfoliata,* rather than throughout its range. The introgressive populations have a survival value due to greater adaptability which enables them to be successful outside the ecological niches occupied by the parent species. When they are found in new ecological niches they will frequently persist. They may represent the beginnings of potential new varieties, which might eventually lead to new species.

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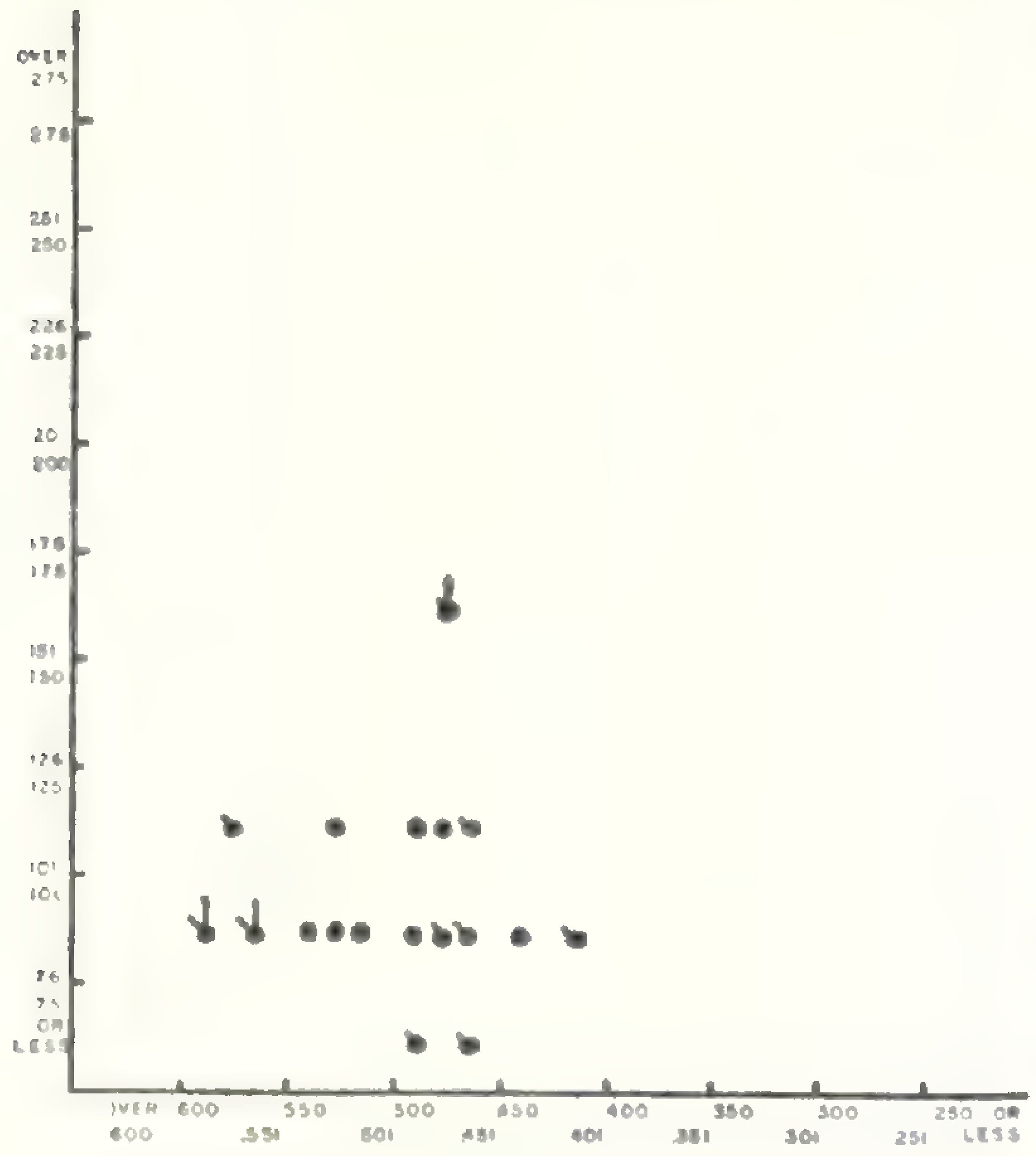


CHART 1 MBG.
PERFOLIATA

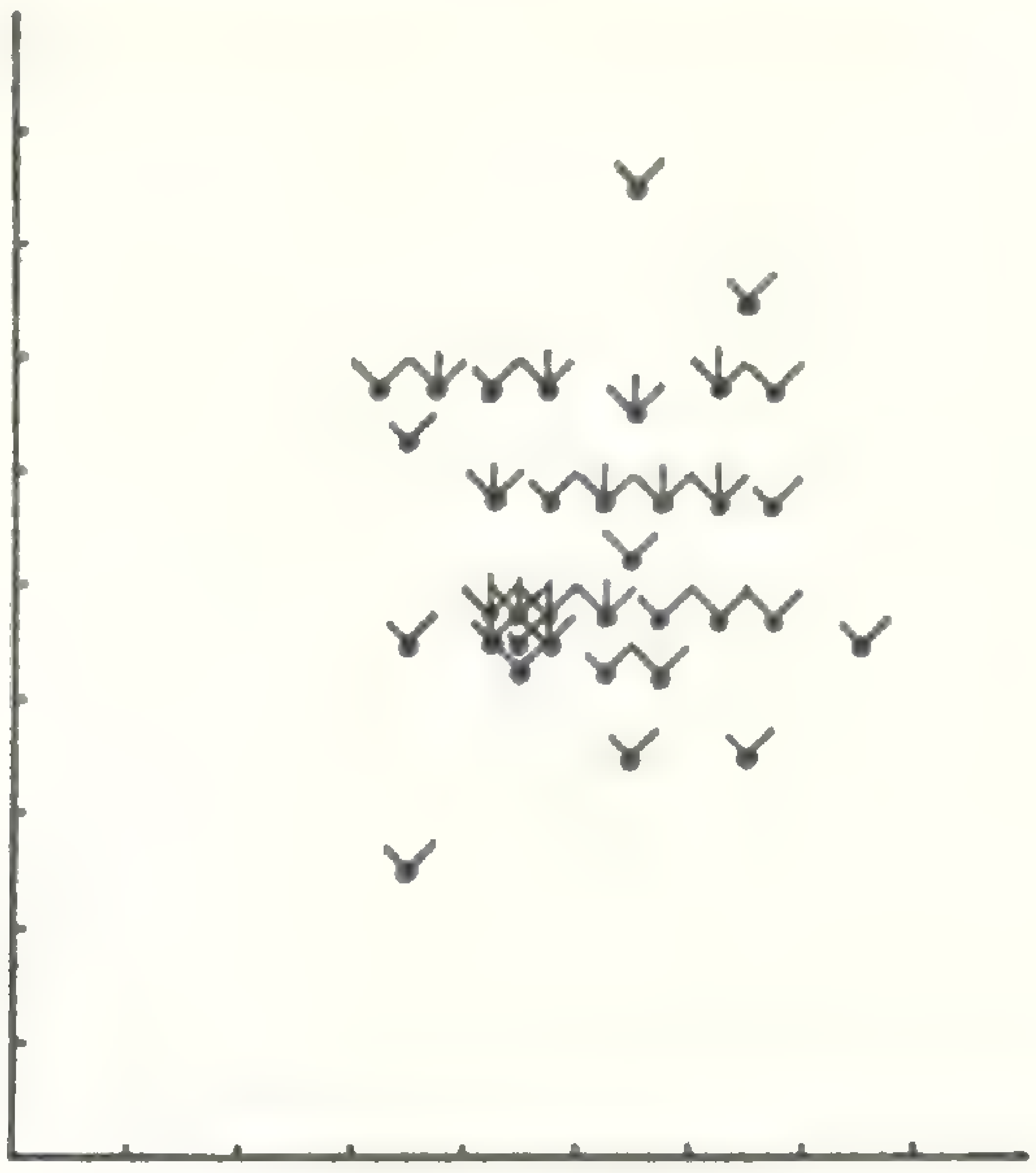


CHART 2 MBG
GRANDIFLORA

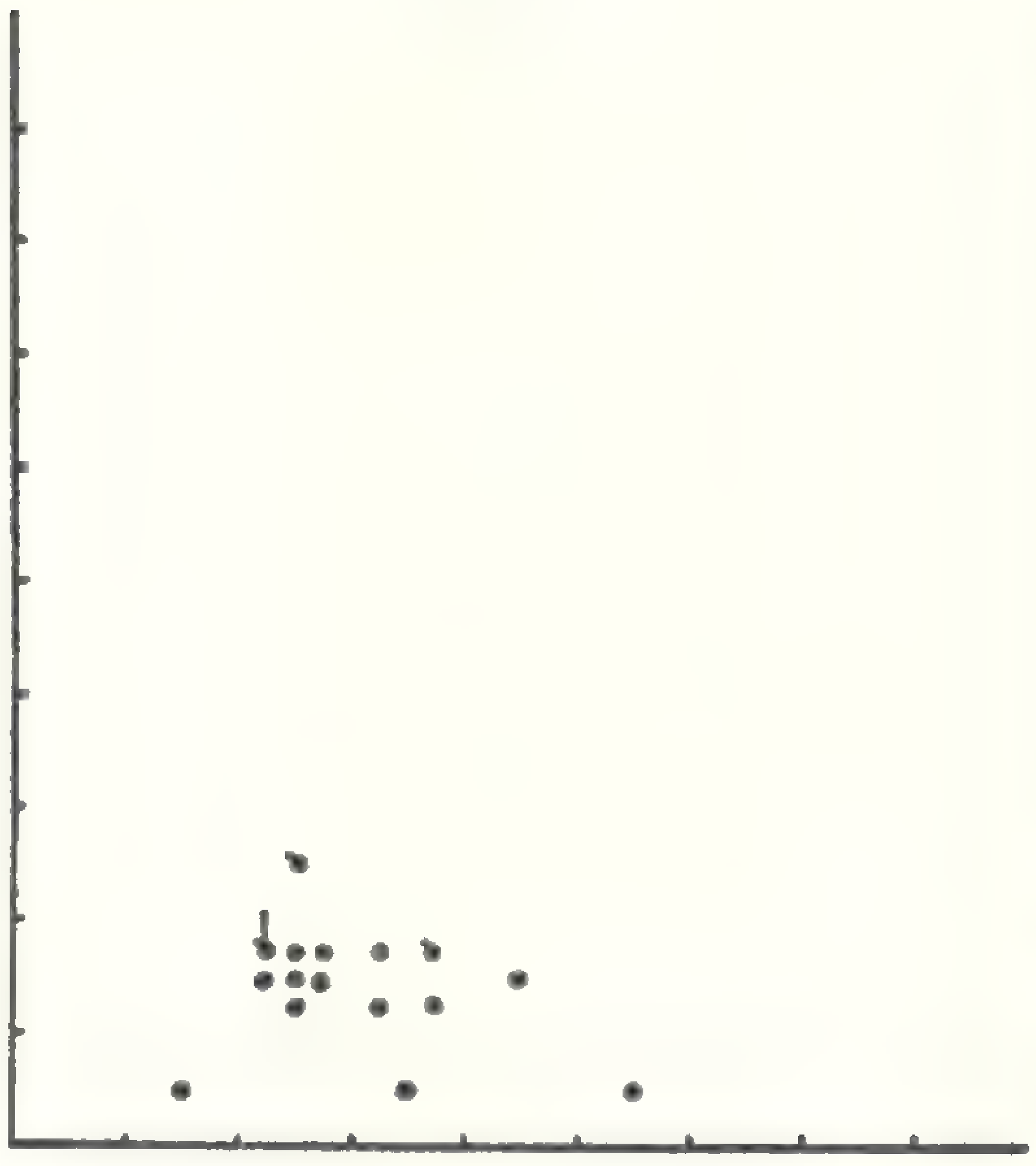


CHART 3 RIDGEWOOD

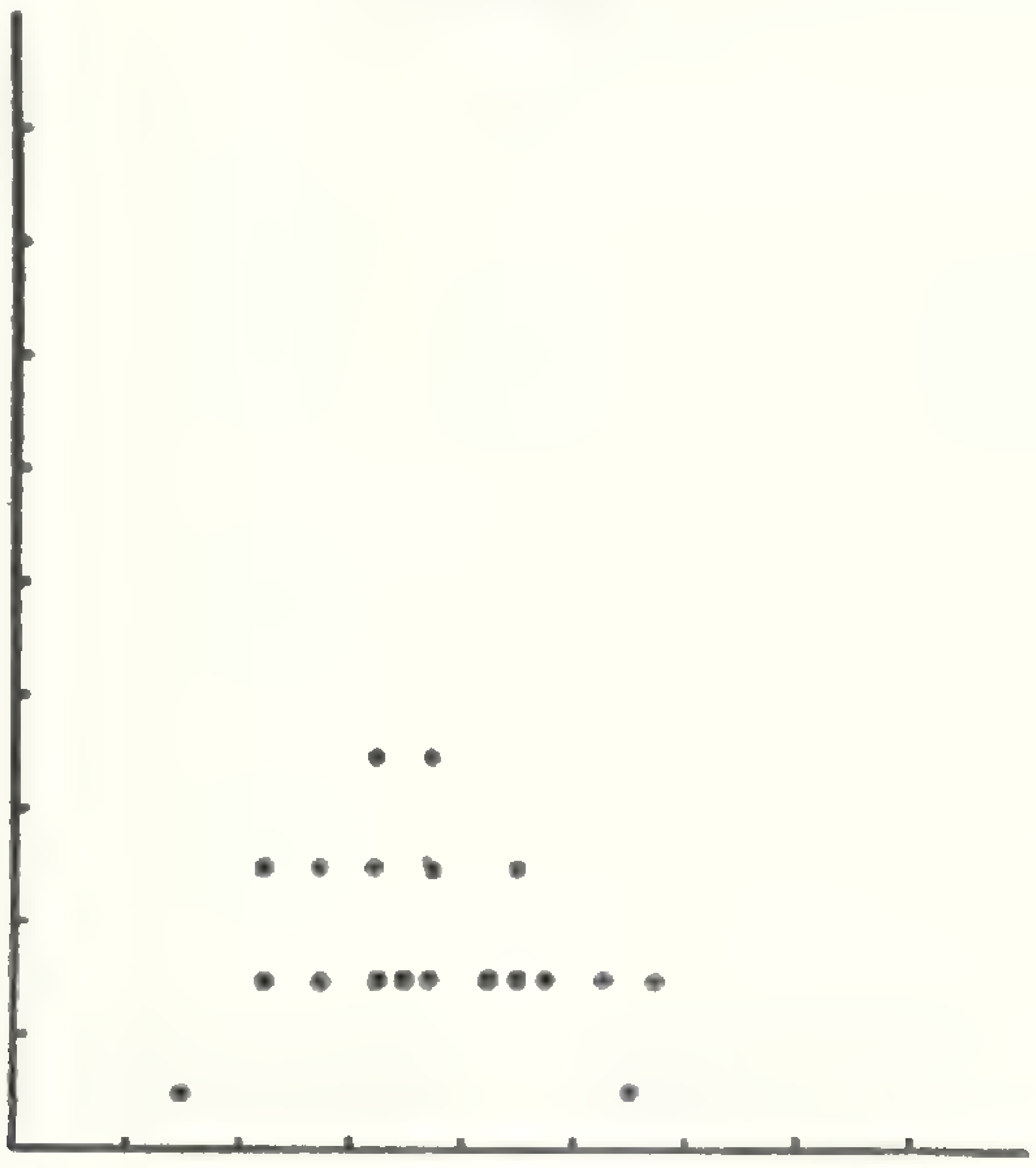


CHART 4 HAWLEY

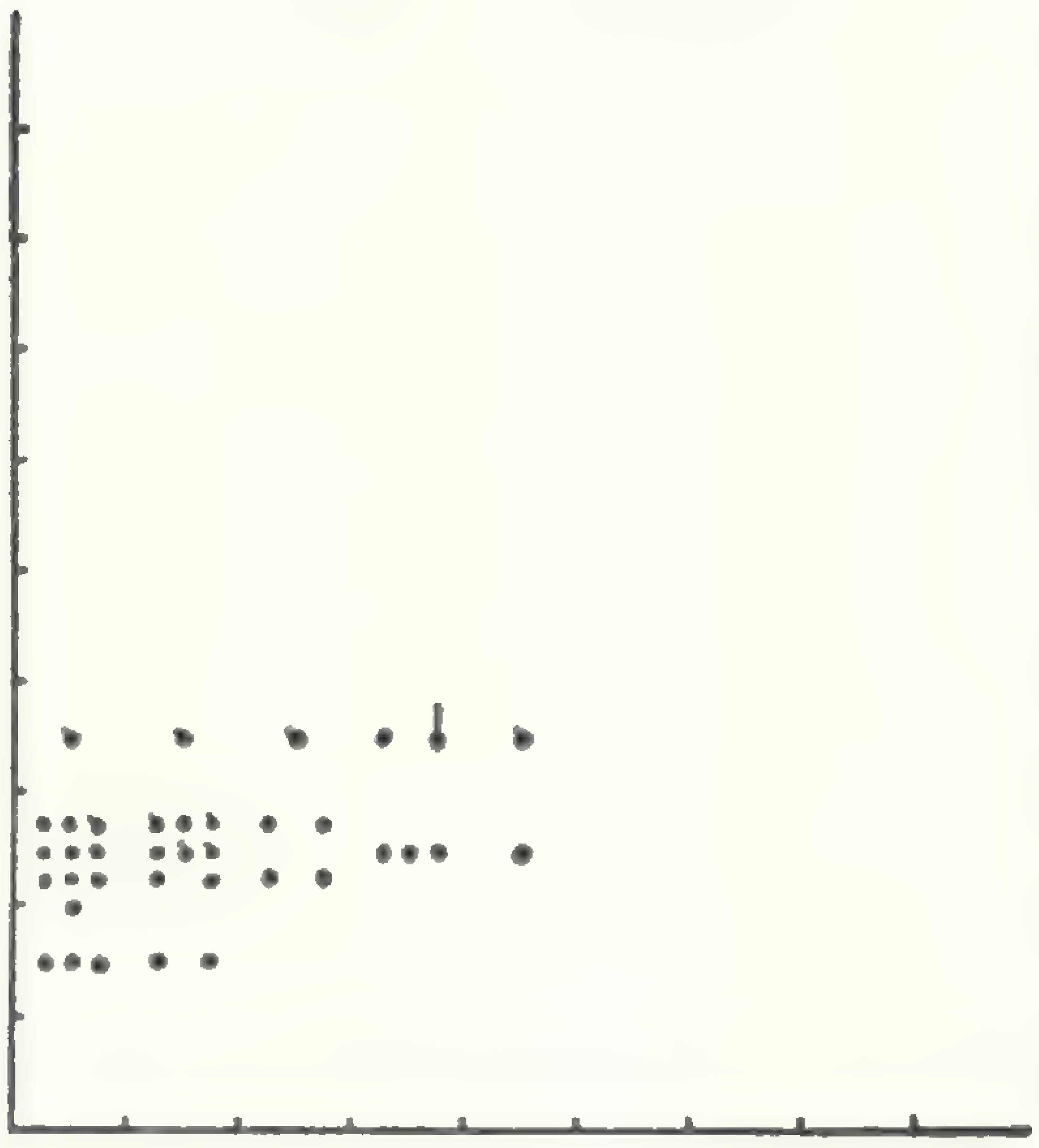


CHART 5 DYESTONE CREEK

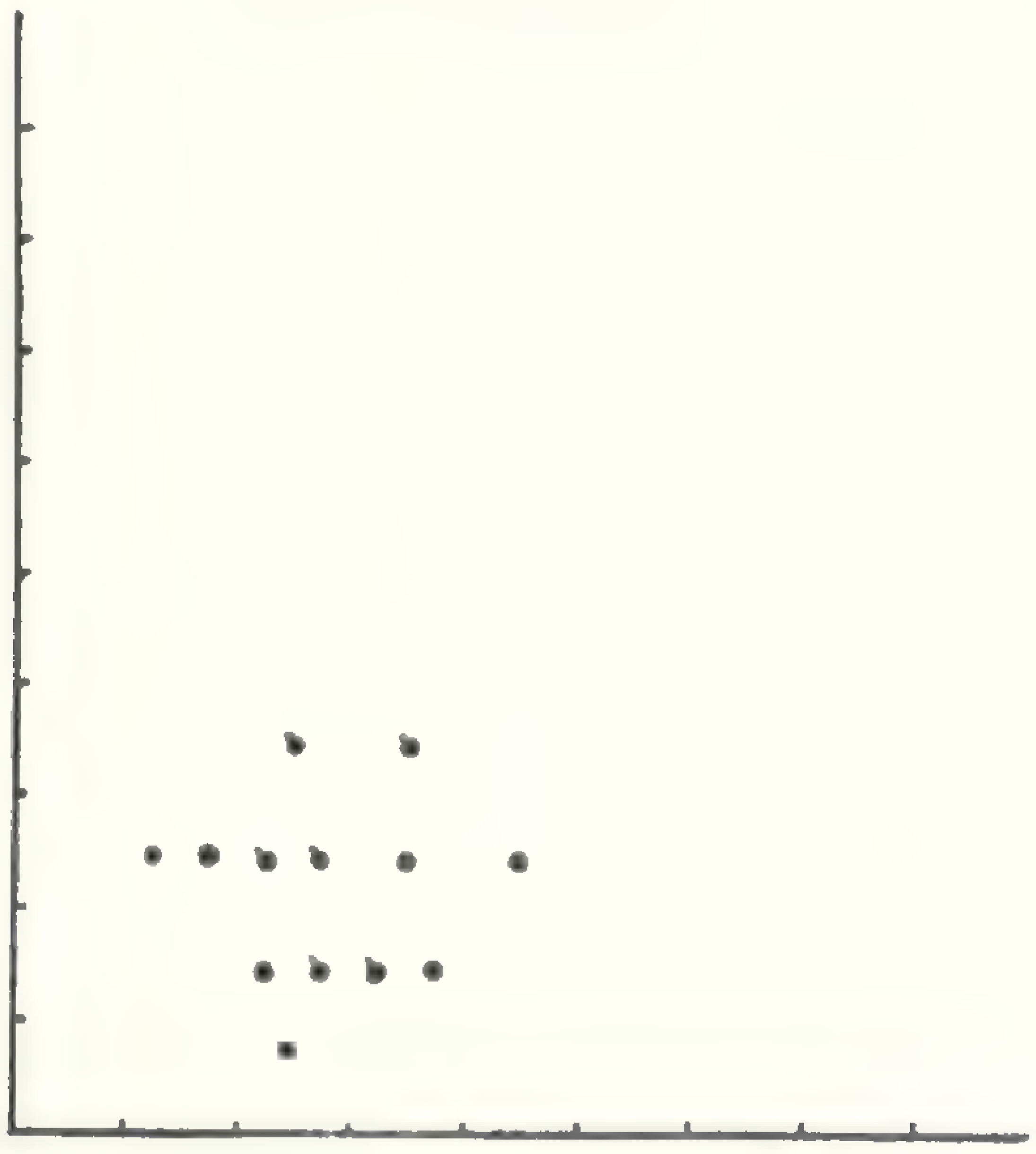


CHART 6 MOUNTAIN LAKE

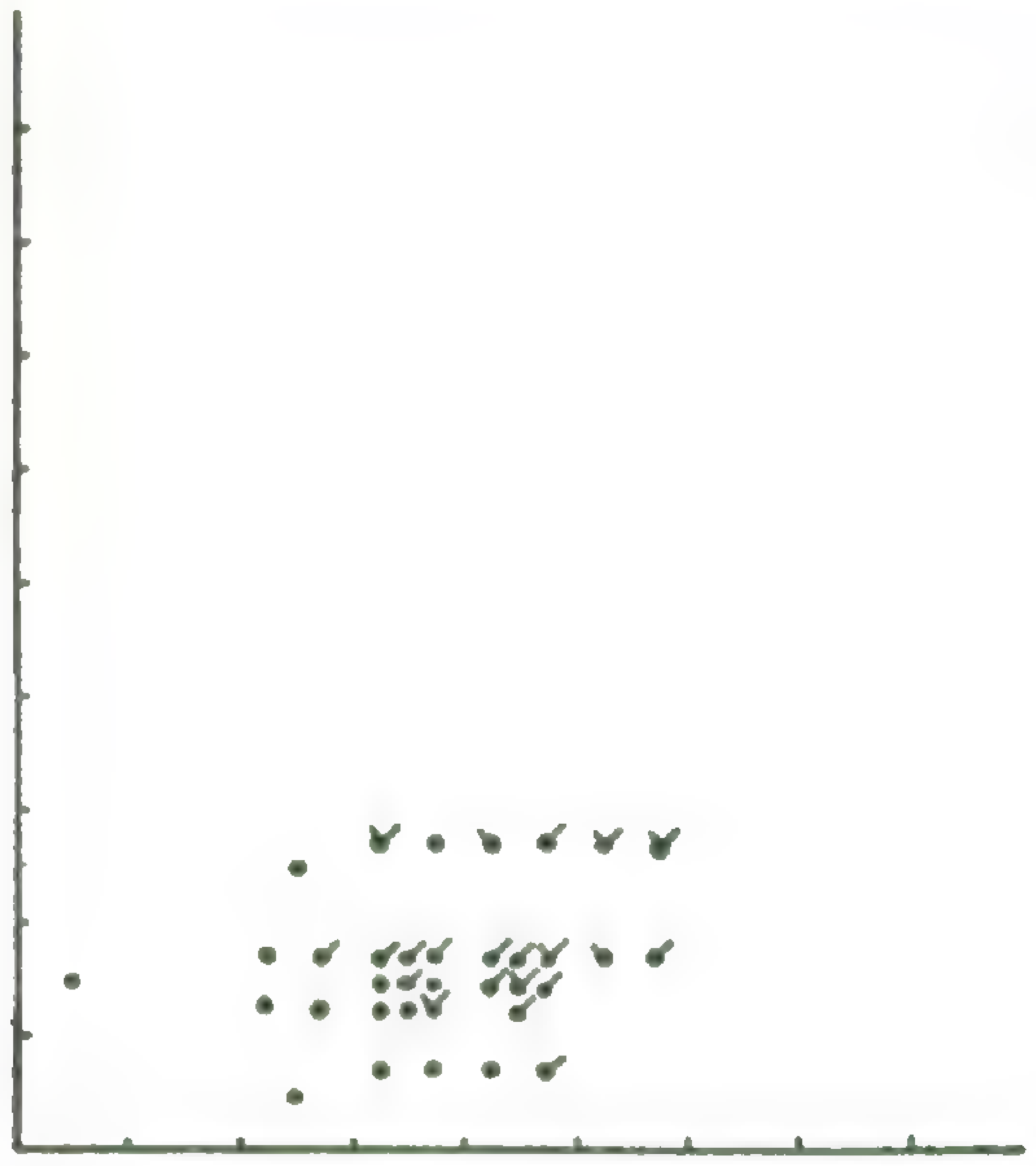


CHART 7 OAKWOOD PARK

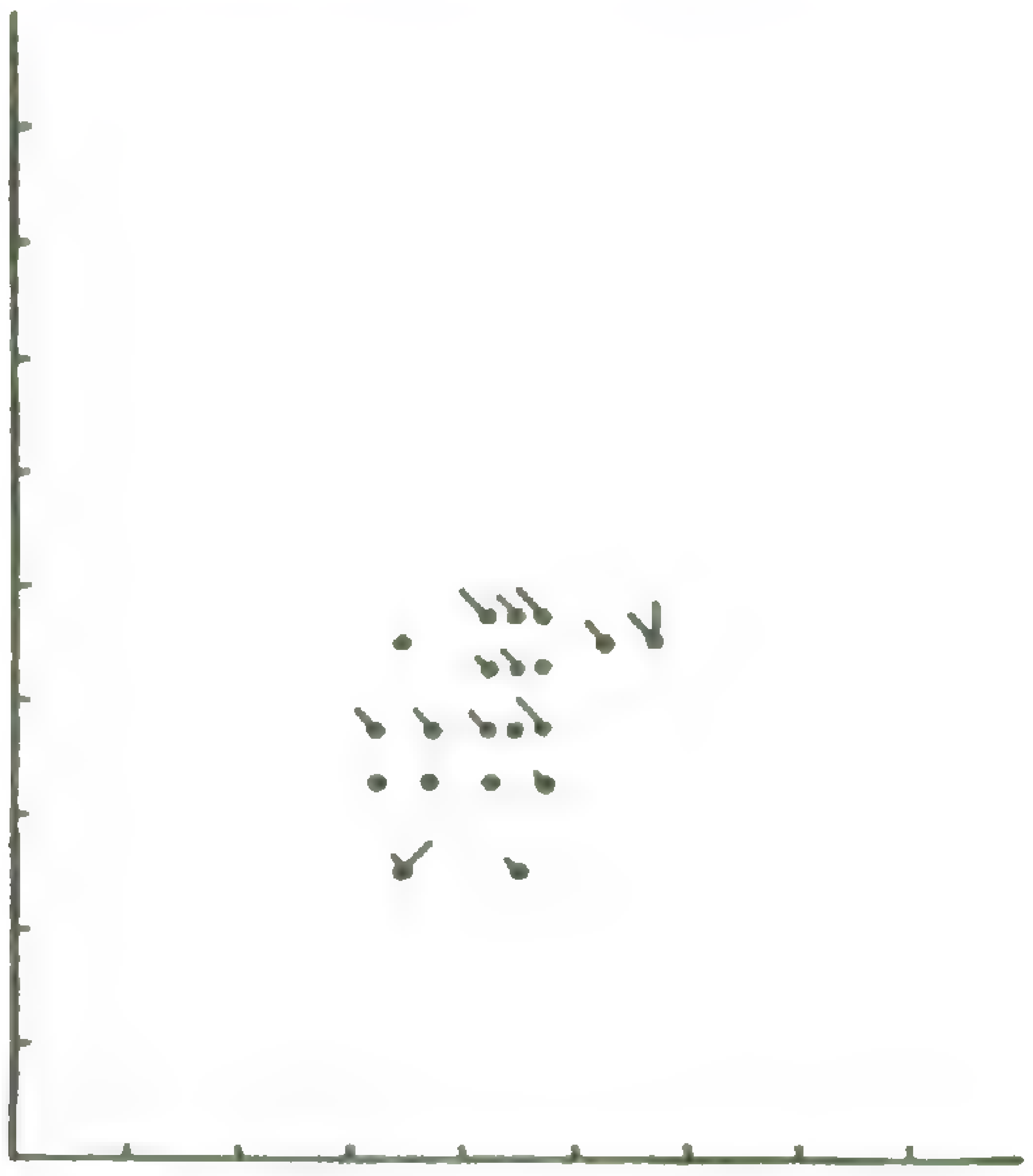


CHART 8 KNOXVILLE "A"

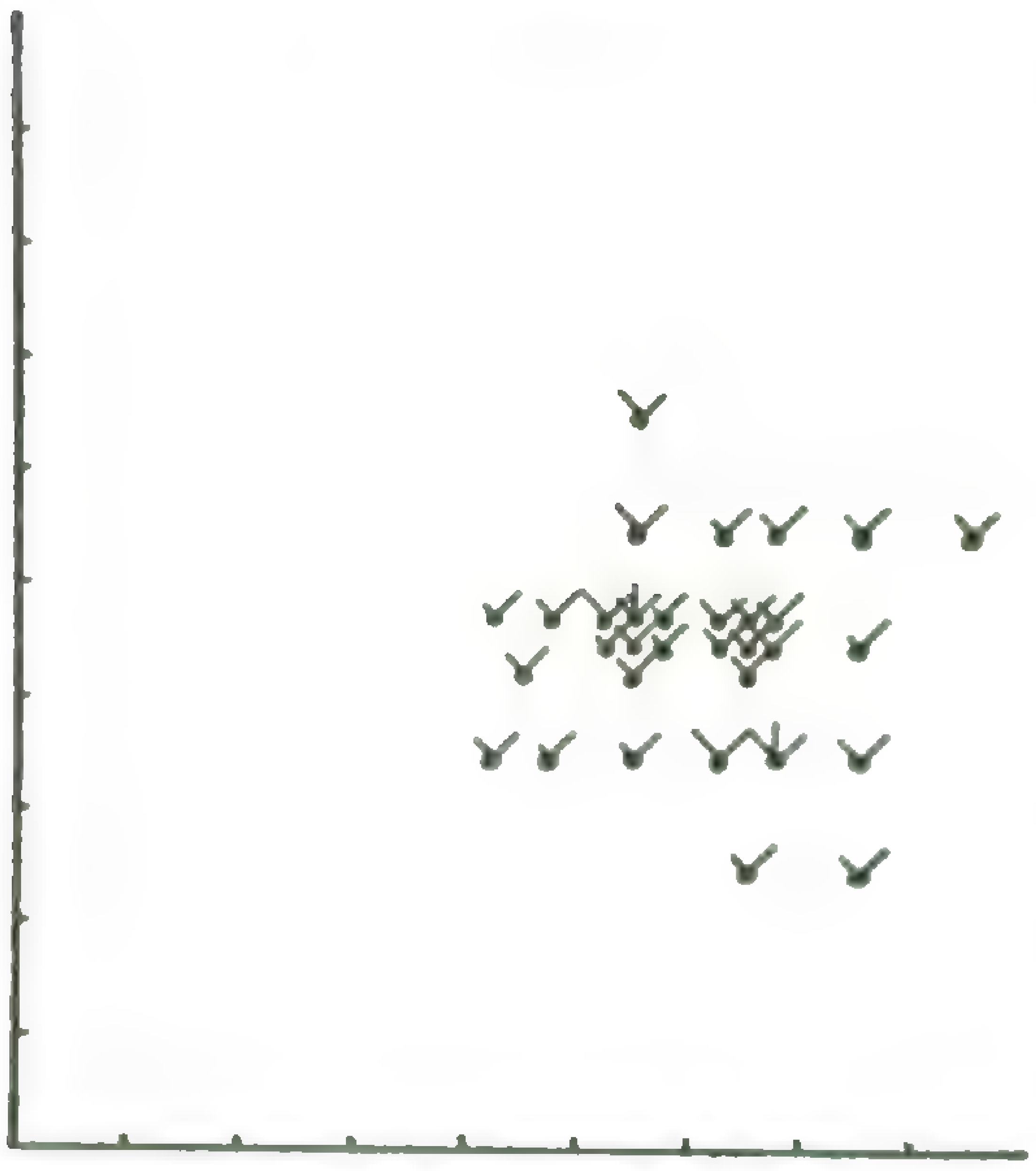


CHART 9 KNOXVILLE "B"

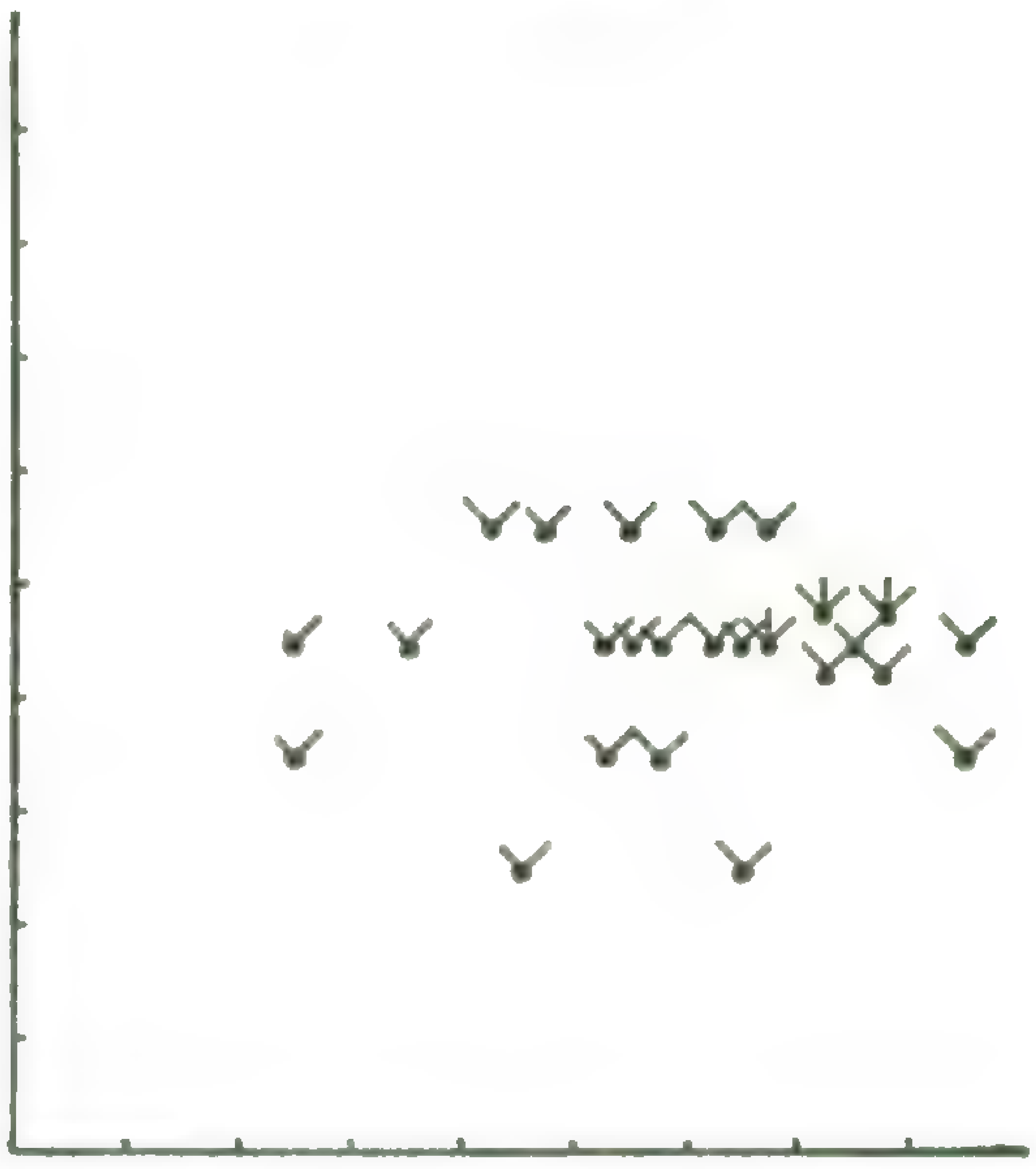


CHART 10 DEBBINK

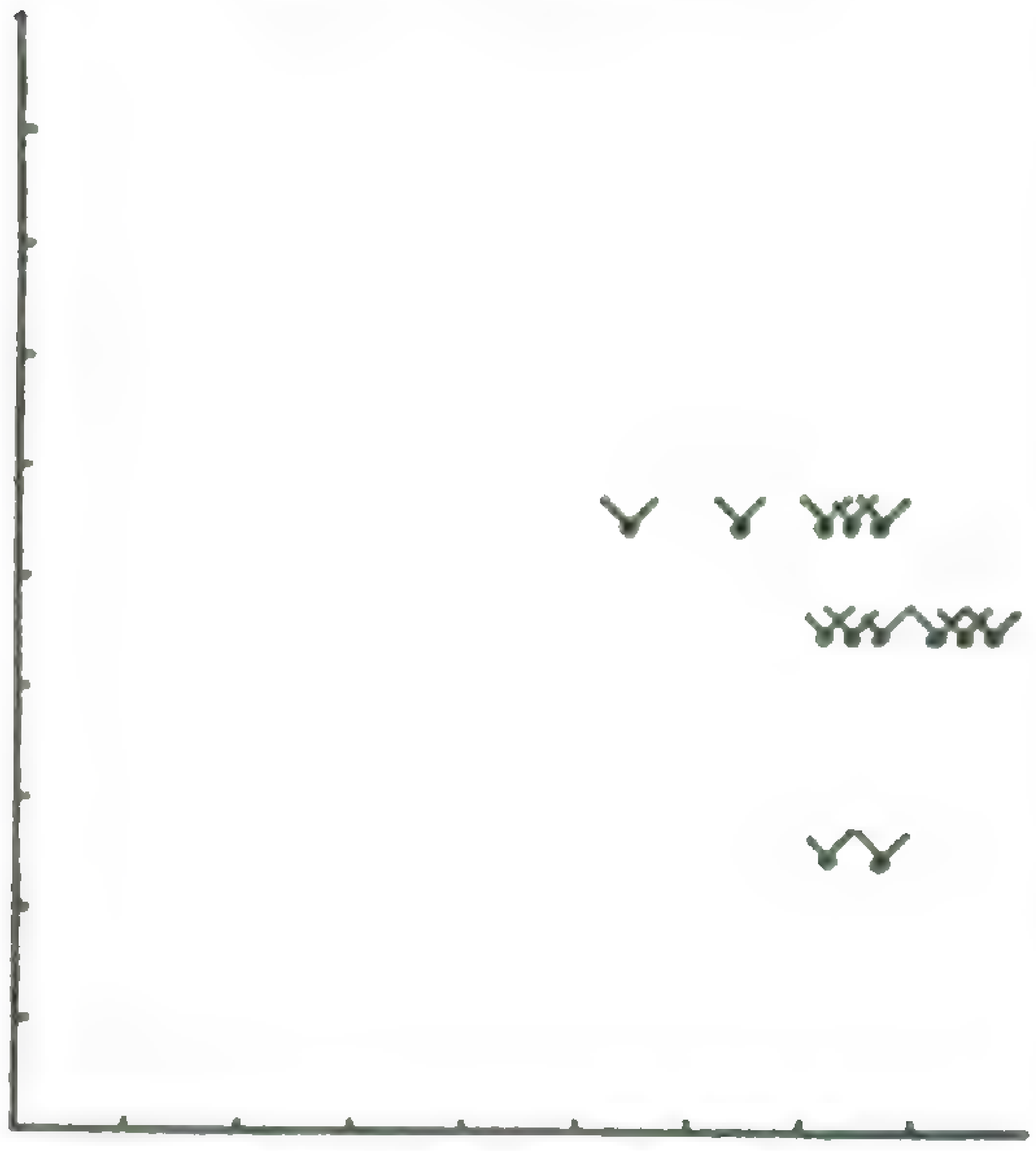


CHART 11 LA BARQUE

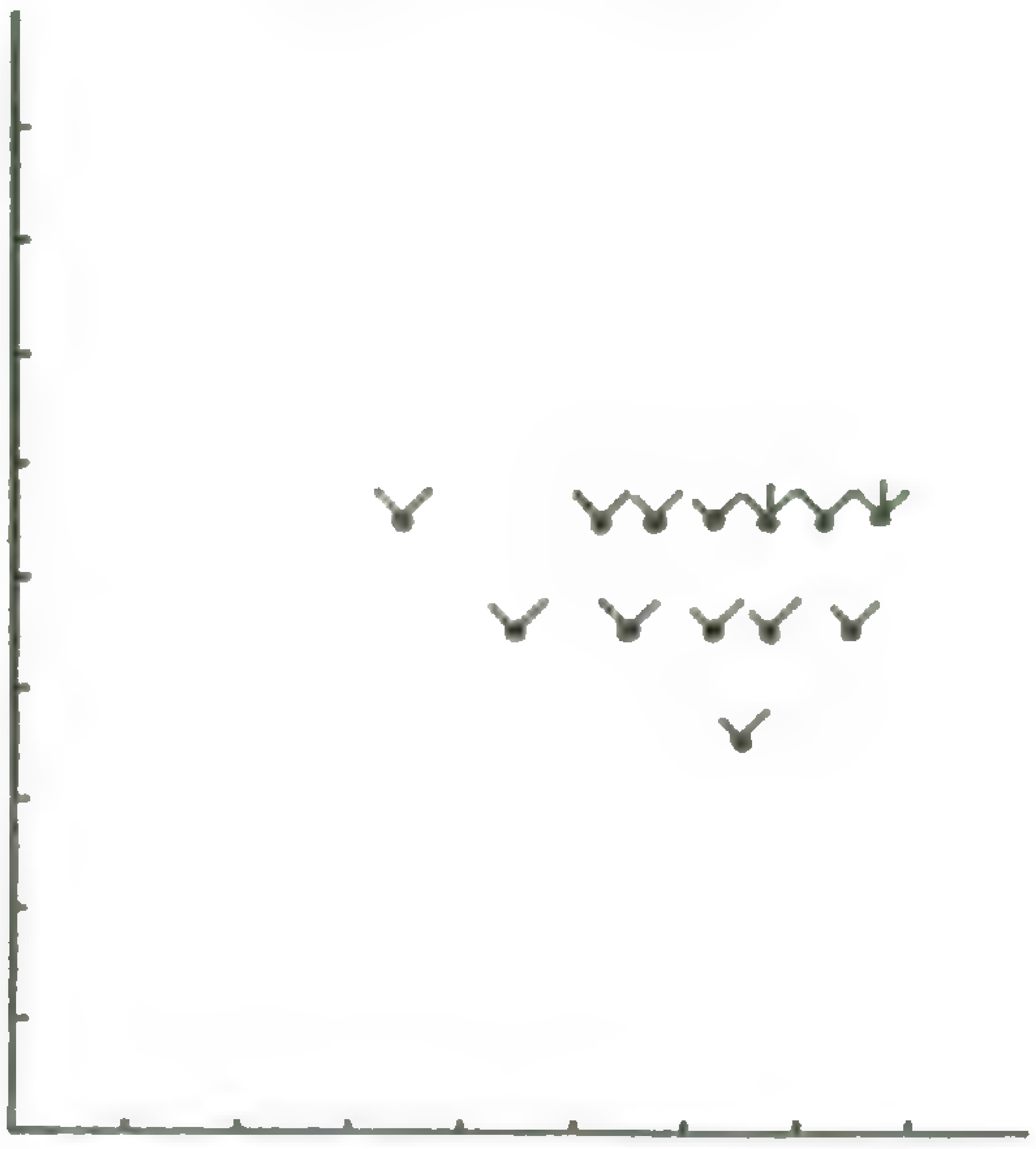


CHART 12 BUTTS

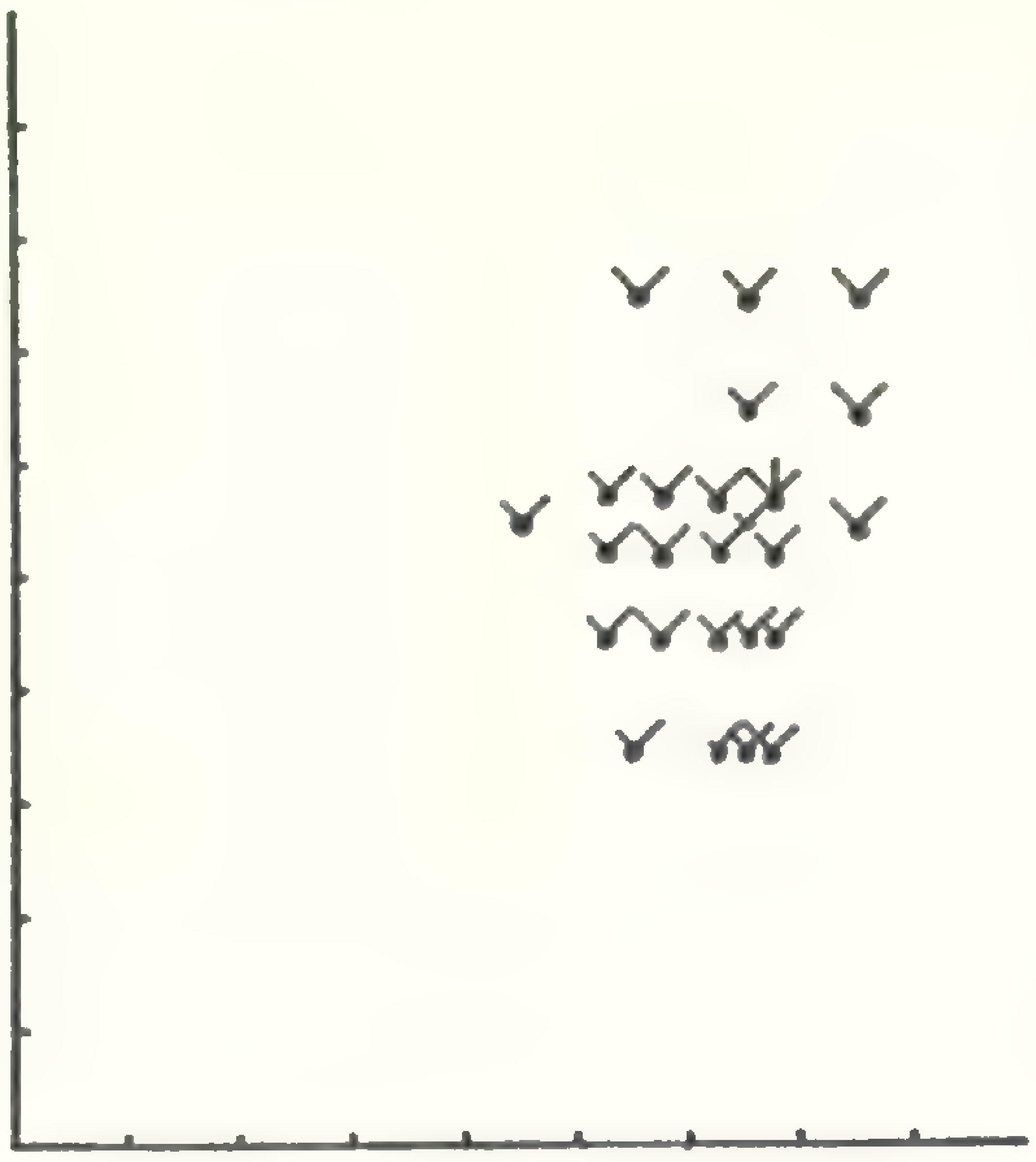


CHART 13 RED LAKE

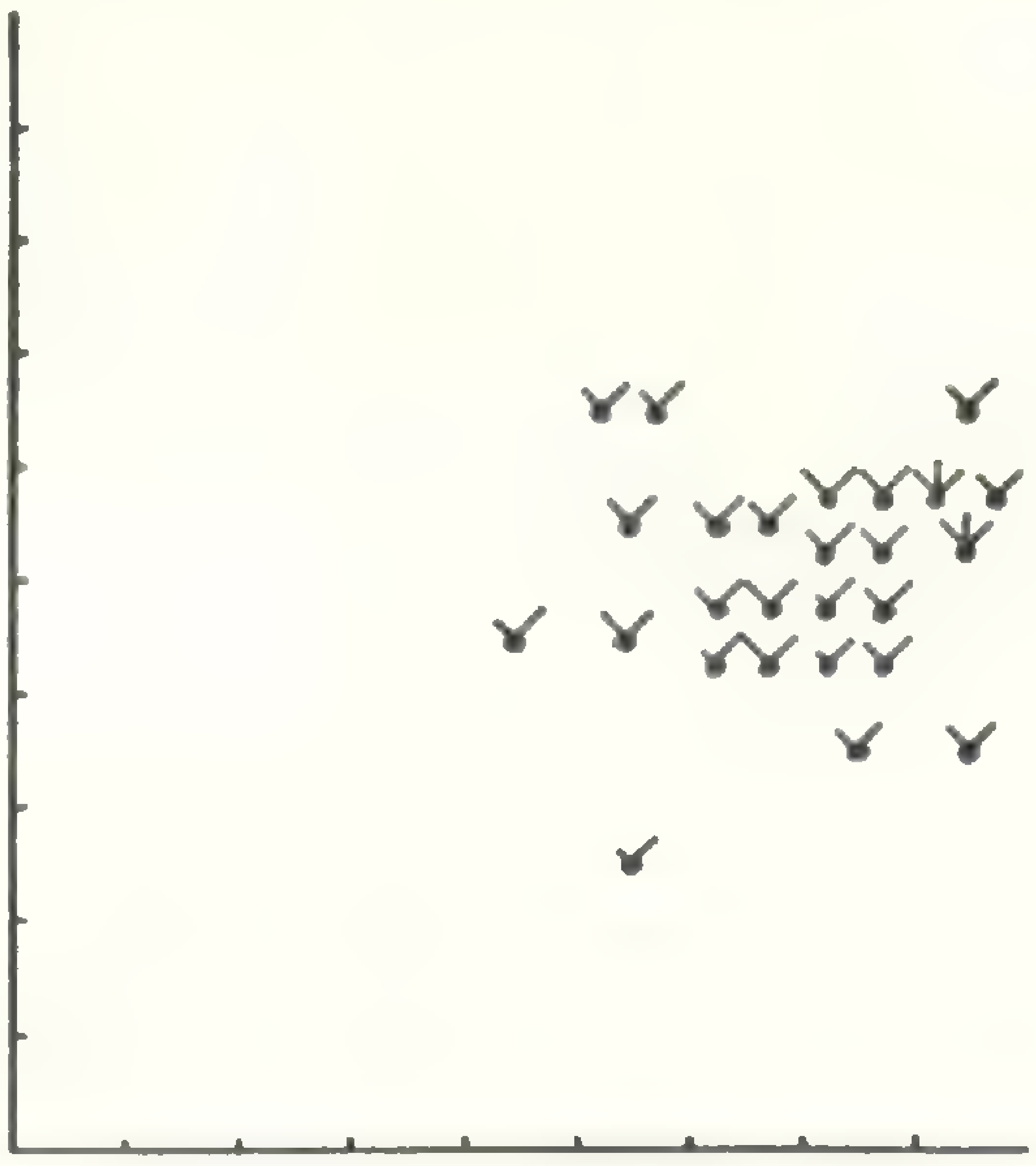


CHART 14 CLARKSVILLE

CHART 15 COXSACKIE

CHART 16 M.B.G. MISSOURI

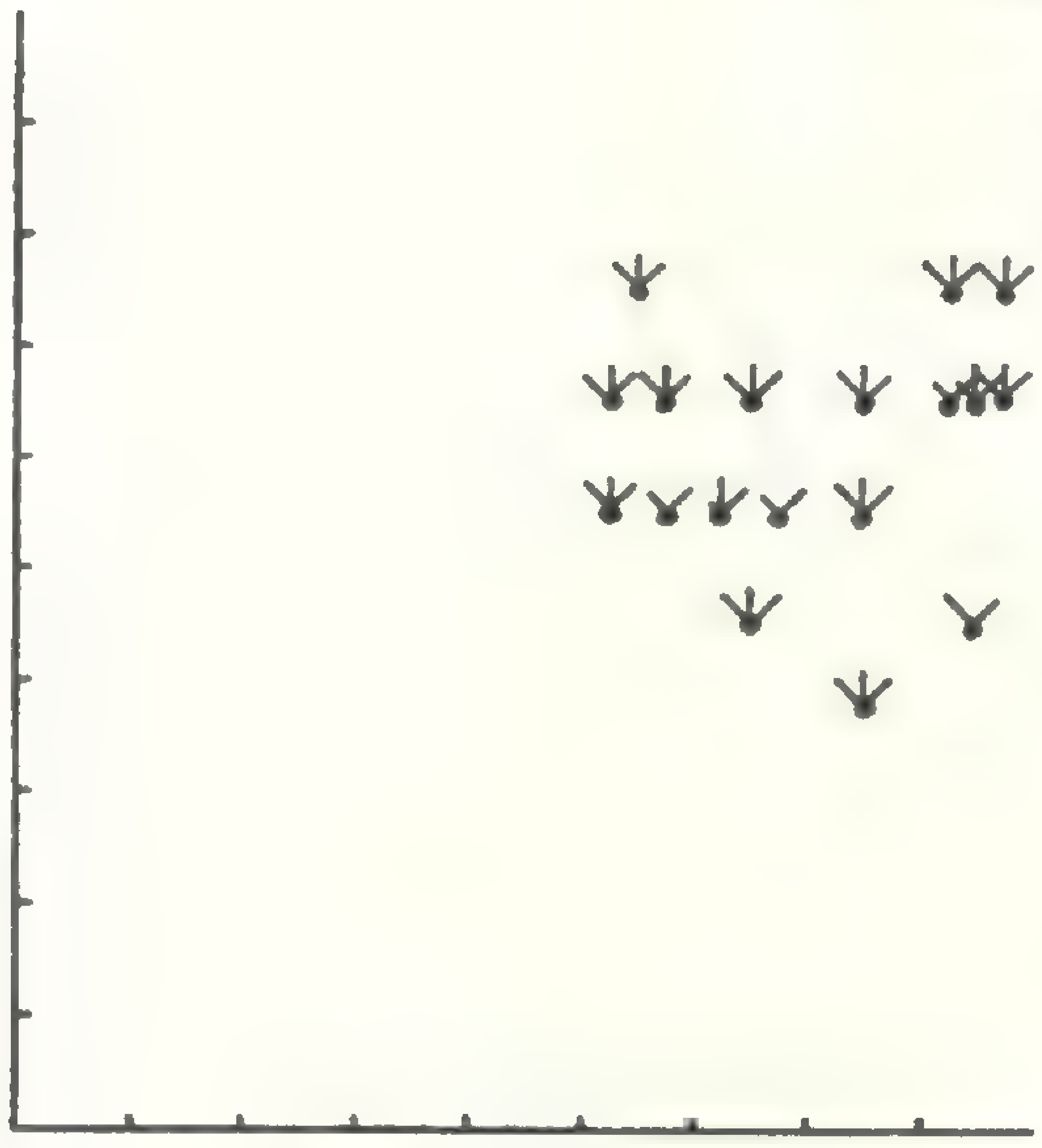


CHART 17 BILLINGTON

THE EVOLUTION OF A GRAVEL BAR

ROBERT A. DIETZ*

One of the characteristic features of many Ozark streams is the occurrence of gravel deposits usually found on the concave bank of river-bends. It has been suggested (Anderson, 1949) that these deposits, known as "gravel bars," may evolve their own flood-control systems. An investigation of one such bar on the Meramec River, at Gray Summit, Missouri, was made in order to determine how the bar had evolved physically, and, in a general sense, how this change affected and was affected by the natural populations of the river bank.

It is generally known that the size and shape of many gravel bars is not constant, but there has been no quantitative work to show this. The determination of the physical changes of this one gravel bar necessitated the assembly of all available historical data, their reduction to a common scale, and the consequent plotting of all recorded changes. This assembly of historical data is not as difficult as it might seem. There usually exist, in offices of county engineers, fairly complete surveyor's reports which may go back 100 years or more, as at the Franklin County courthouse in Union, Missouri. In addition, the field offices of the U. S. Department of Agriculture frequently have large aerial photographs of the areas within their district. Data from these two sources, as well as some private aerial photographs, were used to chart the physical evolution of the gravel bar selected. The data follow:

Record	Date	Source
Survey record	1853	Franklin County Courthouse
Survey record	1881	Franklin County Courthouse
U. S. Geol. Surv. map	1896	Supt. of Documents, Washington, D.C.
Aerial photograph	1927	Missouri Botanical Garden
Aerial photograph	1937	Department of Agriculture
Aerial photograph	1941	Department of Agriculture
Aerial photograph	1950	Made for this investigation
Survey record	1950	Made for this investigation

The records up to 1896 indicate that the Meramec River was without bends or pattern interruptions at the point where the bar is now located. These records are supported by ground reconnaisance, which reveals traces of the old river bed. The north bank of the old river stands out especially clearly (row I in figs. 1–4), marked by a ridge on which there are trees up to 6 feet DBH. The three earliest records coincide in the position of the river, indicating that it probably did not shift significantly from at least 1853 until after the data were gathered for the 1896 geological survey. The 1927 photograph shows a distinct bend of the river, with a crescent-shaped gravel bar on the concave side, as do all subsequent photographs and the 1950 survey maps (fig. 1–4). Consequently, at some time between

*Department of Botany, University of Tennessee, Knoxville.

1896 and 1927, the river embarked upon a period of change with meanders developing in various places.[1]

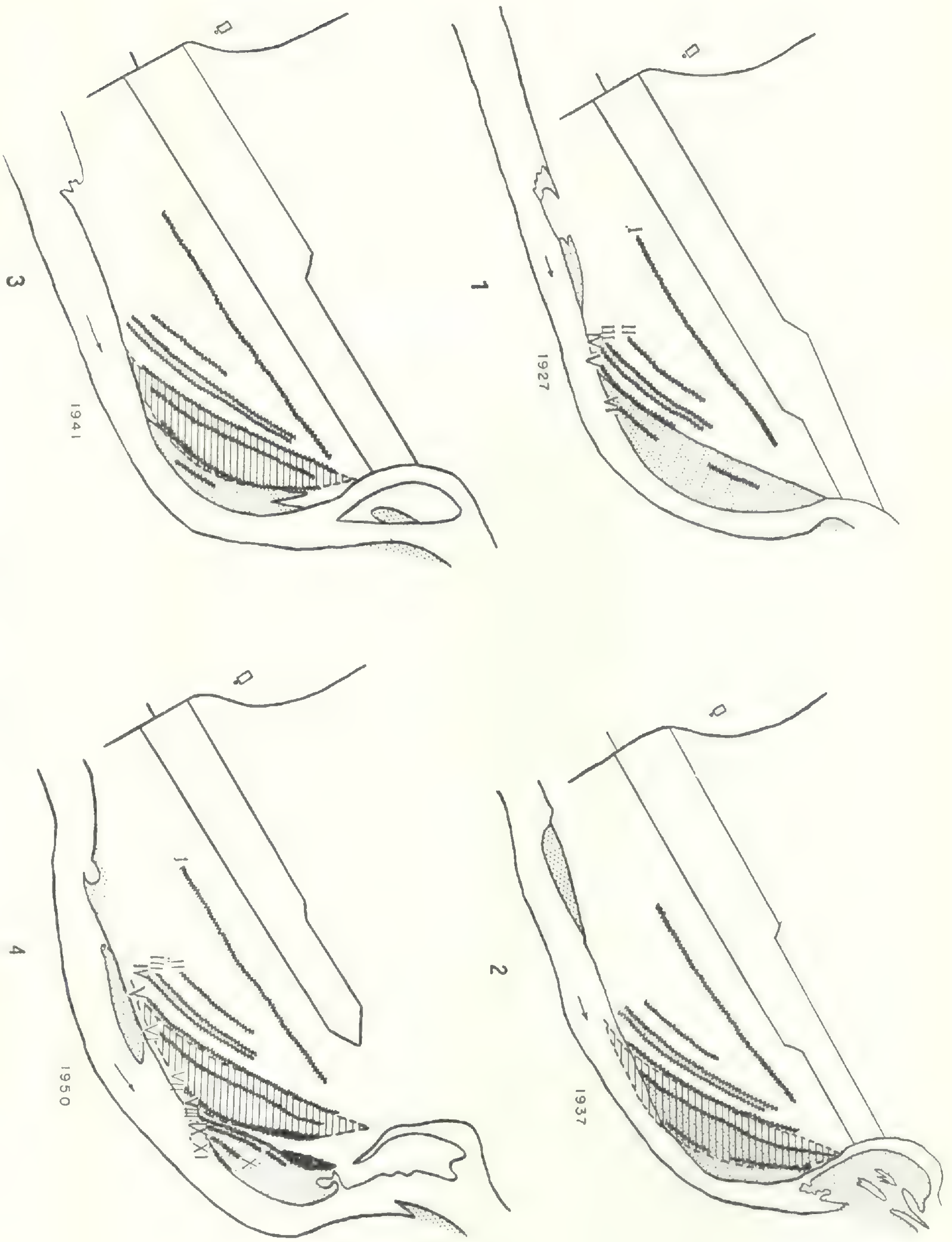
With the assembly of the data, it became necessary to reduce them to a common scale, in order to measure the changes quantitatively. An obvious solution to this problem is to photograph each reconstruction, enlarging the negatives in such a way as to establish final prints with an identical scale for each. In practice, without specialized equipment, this proved impractical. The final prints were very close to being on a common scale—within about 1 per cent—but the small differences between them made the "ground error" somewhere between 50 and 150 feet, too great for the refinement desired.

An alternate method consisted of drawing grids over the original data, with the grid lines a specified and measurable ground distance apart. Charts were then prepared with grid lines constructed equidistant on each chart. The original data were re-drawn onto the prepared charts, and were consequently on a common scale. The transferable error proved to be considerably less than the photographic error described above. Figures 1–4 are outline drawings prepared from four of the final, common-scale charts. These figures show the following facts regarding the physical changes in the gravel bar from 1927 to 1950.

The gravel bar in 1927 was about 800 feet long and 150 feet wide (fig. 1). The dark line marked with the Roman numeral I represents the line of trees along the bank of the former river-bed. In the area transect (fig. 5) these trees are marked with the key-number 12, and the remains of the river-bed with the number 11. By 1937 the bar had moved about 75 feet in a southeasterly direction, and was about 600 feet long and 200 feet wide (fig. 2). In 1941 the inland edge of the bar occupied the same position that the far bank of the river did in 1927. The downstream side of the bar remained about where it was in 1937, but the upstream portion had swung southward about 125 feet. The dimensions in 1941 were about 600 × 100 feet (fig. 3). By 1950 the shift had become nearly due east, so that the gravel bar was nearly 200 feet east of its 1927 position, and was about 500 × 110 feet in area (fig. 4). The same bar in 1952 showed marked changes since 1950. It was wider and more nearly hemispherical, and the fish-shaped bar which appears upstream in fig. 4 has extended downstream until the two bars have almost merged.

As a result of this investigation we now had available quantitative data on the physical changes of one gravel bar covering a period of twenty-three years. If we accept the supposition that the bed of the river prior to 1896 was indeed adjacent to the line of trees designated by the number I on figs. 1–4, as seems likely, then the river must have moved southward a distance of about 350 feet at the point where the upstream portion of the gravel bar was located in 1950, and

[1]Kirk Bryan (1941) proposed cycles of aggradation and degradation by the rivers of the southwestern United States. Is our cycle hololologous with his? There are no data and we can only speculate. Etter (1949) reported an occurrence on a creek in Pike County, Missouri, which adds some fuel to such speculation.



Figs. 1–4. Dot shading shows current gravel deposits; line shading shows 1927 bar location in subsequent years. Further explanation in text.

developed a meander—on which the bar is located—back to, and a little beyond its old course in the intervening half-century or so.

Although this investigation was primarily concerned with the story of the physical change of the gravel bar, the action by the river has had a profound effect on the ecology. A critical observer on the spot, even without prior information on the spbject, can discern without difficulty that willows play an important part in the over-all story of the gravel bar. These shrubs and trees bear directly upon the physical evolution of the bar itself, and the land area behind it.

During the late spring and early summer, when the willows are in fruit, the river surface may be covered with the cottony floating seeds. Willow seeds are viable for only a short period of time, about three or four days according to the U. S. Dept. Agr. "Woody Plant Seed Manual." If conditions are right, some of these floating seeds may give rise to a new line of willows at the water's edge. Briefly, the "right conditions" appear to be these: (1) the river receding after a flood, but still slightly higher than normal, and (2) viable seeds being left on the gentle slope of the moist shore line by the retreating waters. If the seeds remain moist they may germinate, and if the river does not again flood and tear the seedlings out before they have become established, within a few months they will become small saplings. After they have become established, even severe floods fail to dislodge them. The result is a line of willow saplings at the water's edge. In the late spring of 1949 conditions were right for the establishment of willow seedlings, and the writer observed a deposition of seeds. The next spring there was a row of supple saplings, which, due to flood conditions at that time, were several feet out into the water. An attempt to dig up the saplings, with the aid of a shovel and river action, augmented by pulling from above, failed to dislodge a single one.

At the same time it was observed that the swollen stream was gouging out the substrate on both sides of the line of willow saplings. The substrate among the seedlings was not being eroded due to the cohesive action of the willow root systems, but on the contrary, the aerial stems of the willows were slowing down the rate of flow through them to the point where sand and silt were being deposited along the line on which they were growing.

As one walks away from the shore line, several lines of willows may be seen, each on a ridge, with channels between them gouged out by flood action. These lines of willows were apparently deposited in the same manner as described above, and therefore represent the shore line of the gravel bar in times past. Ring counts substantiate this hypothesis. In 1950, seven-year-old willows were found in a line approximating the 1941 shore line, and 10-year-old willows formed a line slightly inside the 1941 shore line.

Three species of willows were involved in the gravel bar studied—*Salix interior (S. longifolia)*, *Salix caroliniana (S. longipes* var. *Wardi)* and *Salix nigra*. For the last species, only one deposition occurred, apparently before 1935, but the other

two had occurred at intervals over that same period. The lines on the map (fig. 1–4) correspond to observable rows of trees. The line marked VIII was largely S. *interior,* that marked IX was largely S. *caroliniana.* Line VII contained S. *nigra, Acer saccharinum, Ulmus fulva, U. americana,* and *Populus deltoides.* Inland from line VII there were no willows. In this area the ridge furrow topography is occasionally preserved, although discerned only with difficulty. Those which are observable are marked on the illustration (figs. 1 and 4) with Roman numerals. The numbers run from I (the presumed bank of the river during the nineteenth century) to XI (the water's edge in 1950). These features tell the story of successive changes in river position since the change began. Figure 5 shows a cross-section of the area from the middle of the gravel bar northwest to the old river bank. Well-developed stream-bend gravel bars present an example of spatial succession, similar to that observed in such places as the dunes region of lower

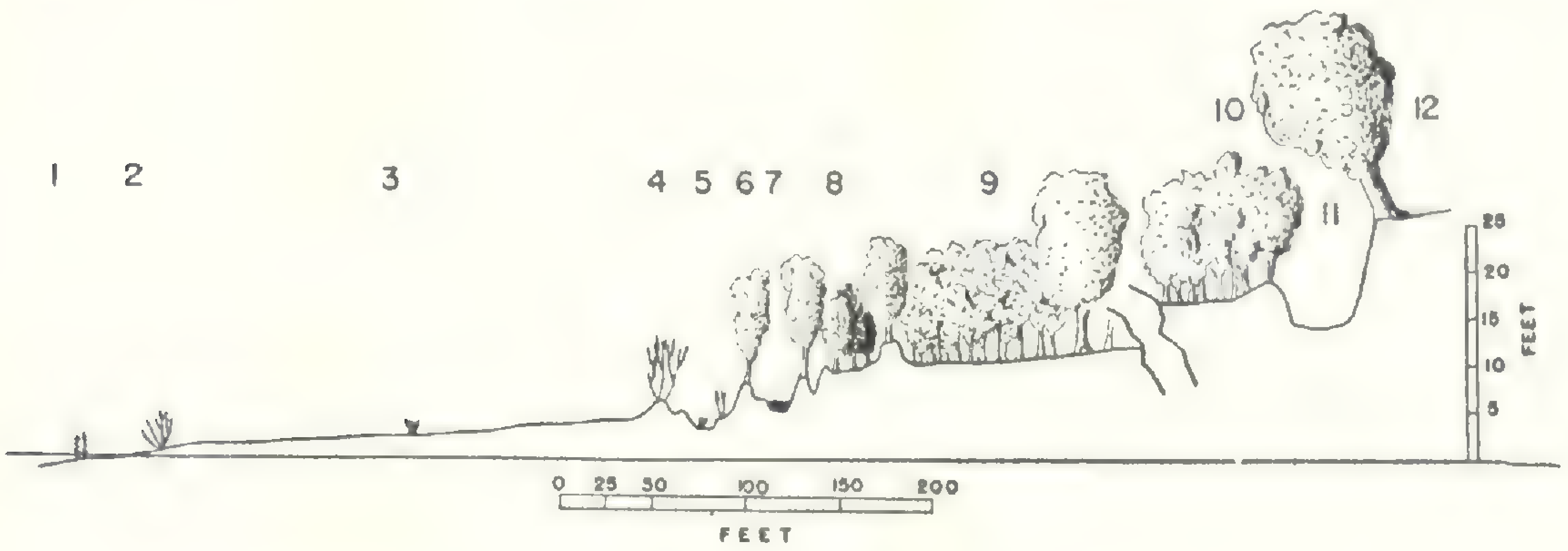


Figure 5. Explanation in the text.

Lake Michigan. In fig. 5, from the water's edge inward, we see: (1) Water Willow, *Dianthera americana,* a transient plant which is ripped out by severe floods; (2) willow seedlings of various species, the first permanent plants; (3) the strand, generally barren gravel and sand, on which the permanent plants are willows, *Amsonia illustris,* and *Panicum virgatum;* (4) and (6) ridges on which are large willows; (5) and (7) fosses or canals, gouged out by flood action, in which *Panicum* and *Amsonia* are permanent residents, as on the strand, although in the fosses they tend to slow down the flood water, resulting in the eventual filling up of these areas by deposition; (8)–(10) the area in which willows are replaced by cottonwoods, elms, and maples, roughly in that order; (11) the old river bed; and (12) the row of large old sycamores, maples, etc. making up the old river bank.

Since the three species of willows growing on this one gravel bar generally flower at different times in normal years, there are three chances during a year for conditions to be such that a line of willows could become established. Ring counts of the oldest solid line of willows (Ridge VIII) indicate that seeds for these were deposited in 1940. In the ten years from 1940 to 1949, inclusive, there were thirty chances for willows to become established. Actually, only four lines were successful, although some lines contain two species, indicating a seedling success rate of

about 13 per cent, at least as far as the establishment of a new physical line is concerned.

As previously noted, Anderson suggested that some gravel bars evolve their own flood-control systems. The writer's observations indicate that such appears to be true of the bar studied. In times of flood the water is spread out and channeled through the fosses. Those farthest from the river eventually become choked up with plants, but in the fosses of intermediate distance only such plants as *Amsonia illustris* and *Panicum virgatum* can exist through flood periods. Like the willows on the ridges, these plants are not torn out by severe floods, and they seem to serve to slow down the rate of flow in the furrows as the willows do on the ridges. More of this slowed-down, channeled water seeps into the ground, and run-off is lessened. In 1949 beaver *(Castor canadensis)* made use of one of the fosses, damming it up and creating a small pond behind it. The dam has survived several floods. By 1952 the beavers had moved on to another area, but their dam still serves to augment the other natural flood-control features of the gravel bar area.

SUMMARY

A gravel bar on the Meramec River at Gray Summit, Missouri, has been studied from the standpoint of changes in shape and location. Maps and aerial photographs covering a period of 97 years were employed. From the first record of a gravel bar on a 1927 photograph until 1950, the evolution of this bar has been studied quantitatively. It has changed in size from about 800 × 150 feet to about 500 × 110 feet. It has changed in position to a point about 200 feet east of its former location.

These changes are confirmed by an analysis of the ridges and fosses on the surface of the bar and the adjacent areas. These features are caused by the resistance of willow saplings to dislodgement when once established. This leads to the development of a ridge and fosse topography which provides natural levees and spillways for the river. Since the willows are originally laid down on the shore line, we have a record in the ridge and fosse topography of the changing shore lines over a period of years.

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Volume XXXIX Number 4

Annals
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PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price ————	$10.00 per volume
Single Numbers ————	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Annals
of the
Missouri Botanical Garden

Vol. 39 NOVEMBER, 1952 No. 4

A SKETCH OF THE HISTORY OF FERN CLASSIFICATION

ROLLA M. TRYON, JR.*

During the two centuries since the beginnings of formal classification the group of ferns has grown from less than 200 to approximately 10,000 species. Against this background of ever-increasing knowledge, augmented later by the theory of evolution, the classification of ferns has developed. With the considerable present-day interest in the ferns from the viewpoints of paleobotany, anatomy, cytology and morphogenesis, as well as systematics itself, it is certainly desirable to understand our present classification, its basis and its problems. While these might be stated categorically, they can only be understood in the light of their history. Although J. E. Smith (1810), John Smith (1875) and Jean-Édouard Bommer (1867) have, among others, published good reviews of the earlier fern classifications, it will be desirable to follow these again as well as the more recent developments. One cannot, in a brief review, mention all of the authors who have contributed materially to our present classification of ferns nor is it even possible to do justice to the few selected. Rather, I will trace the more important trends in classification and mention some of the most significant authors and their works by way of illustration.

On the authority of Sir J. E. Smith we may pass by the seventeenth and early eighteenth century authors, for as he has said (Smith, 1793, p. 401[1]): "The Genera of Ferns, entirely neglected by the older botanists, and but slightly or superficially touched upon by systematic writers of the last century, were first attempted to be reduced to fixed principles by Linnaeus." The shape of the sorus and its position on the leaf afforded Linnaeus (1753, 1754) the primary characters for his genera. He recognized 11 genera of Filicales[2] in his Cryptogamia Filices and about 175 species. This was a highly artificial arrangement, species of quite distant relation

* Assistant Curator of the Herbarium, Missouri Botanical Garden.

[1] In this and the next quotation the reference is to the original paper, but the quotation is from the English translation (1798).

[2] The works to be discussed differ considerably in their scope—some are complete, some omit one family, others omit several families. As a matter of convenience, the number of genera given for each classification is that of the Filicales as presently defined, i.e., the Leptosporangiatae. All authors include the largest family, the Polypodiaceae, *sens. lat.*, and the inclusion or omission of the smaller families does not greatly alter the comparative value of the numbers.

being placed together, yet it was a beginning and served a utilitarian purpose in placing newly described species until it was succeeded by a more natural system. It was not that Linnaeus' characters were at fault, for we still use them today, but rather that they alone are quite inadequate to establish natural genera.

Characters of the indusium were first used effectively by Sir James Edward Smith (1793) some 40 years after Linnaeus. Smith recognized 20 genera based on characters of the shape of the sorus, its position on the frond, the shape and placement of the indusium and the manner of its opening. He expressed his views on the importance of the indusium, particularly the manner of its opening, in these words (Smith, 1793, p. 405): "This circumstance no one has yet considered; yet it is undoubtedly of the greatest use in determining natural genera, being not only constant in every species, but in ferns whose habit and other particulars agree, it is always found to be similar." Smith's classification is also the first to be presented as a natural system. Since his time authors have basically agreed on the need for a natural system but beyond this there has been, as we shall see, much diversity of opinion. It would probably be difficult to improve on Smith's system so far as the species he knew are concerned. However, in retrospect we can see that he underestimated the group he was classifying by using only characters of the fruiting parts to define his genera.

The first handbook of ferns, by Olof Swartz (1806), treated 33 genera and something less than 700 species. Swartz used the same characters of the sorus and indusium as established by J. E. Smith, and his book represents the first fully elaborated treatment of Smith's system. In spite of the fact that many of Swartz's genera were large and unnatural, they were accepted until three decades later. In the interim new genera were described, but on the same basis as before. One of the most elaborate classifications following the Swartzian system was published by Niçaise Augustin Desvaux (1827). He recognized 66 genera of Filicales, an increased number due to a more detailed analysis of characters of the indusium and of the disposition of the sporangia.

Actually, the naturalness of Smith's system was in part passé even before Swartz's elaboration, and it certainly was entirely so by the time of Desvaux's classification. However, the recognition of additional genera based on increased study of the sorus and indusium did make the latter system more natural than Swartz's. It is now fully apparent that new species were being added so rapidly that most genera could not be maintained as reasonably natural groups without splitting them on the basis of new characters. Perhaps one reason that this was so long delayed was that the known ferns could all be conveniently placed into genera based solely on the characters of the sorus and indusium. However usable, this system was finally challenged since too many species, diverse in other characters, were all mechanically placed in one genus.

The notable revision of fern genera by Karel (Carolo) Boriwog Presl (1836) introduced new, essentially modern, principles of classification. He used vegetative characters as well as those of the fructification, placing special emphasis

upon the venation. In addition he used characters of habit, of the rhizome, position of the leaves, number of vascular bundles in the petiole, and the nature of the indument. He discussed and illustrated spore characters, although he did not make use of them in his classification. Presl recognized 117 genera in 1836 and added 59 more in his later publications (1843, 1845, 1852). That generic characters may be drawn from any part of the plant—their value being dependent upon their behavior and correlation with other characters—and that the vegetative organs may furnish characters of equal or even more importance than the fruiting organs became evident in the work of Presl. Although his system has been corrected in many ways his methods are still valid.

Presl must be given credit as the founder of modern pteridology in point of time, but actually this should be shared almost equally with John Smith who worked out a revision of genera independently. Smith (1841-1843), although differing on generic limits, employed essentially the same kind of characters as Presl, generally placing strong emphasis upon venation and vegetative characters. He recognized 138 genera of Filicales. The independent publication of two such similar classifications simultaneously would seem to emphasize that the time was ripe for the introduction of new principles.

The new approach to classification was hardly well founded, however, before it was effectively challenged from an authoritative position. Sir William Jackson Hooker, Director of the Royal Botanic Gardens, Kew, had provisionally accepted many of John Smith's and Presl's genera in his 'Genera Filicum' (Hooker & Bauer, 1838–1842). A few years later (Hooker, 1844–1864), he began publication of his monumental 'Species Filicum'; he comments in the introduction (Hooker, 1:xiv):

> Increased study has, he must confess, strengthened his conviction that those Botanists, who have showed themselves peculiarly addicted to multiplying genera, have not always taken Nature for their guide, nor succeeded in eliciting a simple and tangible arrangement. . . . In these remarks Dr. Presl and Mr. John Smith are particularly alluded to.

Hooker recognized only 63 genera and based them on the classical characters of sorus and indusium. He did not deny the naturalness of many of Presl's and John Smith's genera and treated them as subgenera or sections. In his free use of these subgeneric categories—89 of them—Hooker probably strove for a middle course between the large unnatural established genera and the smaller, relatively natural ones of Presl and John Smith. As we see it now, this was not a particularly successful attempt since in the large genera the section became of equal importance to the genus itself.

There seem to be two basic differences in the viewpoints of Hooker and those of Presl and Smith. Hooker required that genera be based on characters of the fruiting parts (vegetative characters were of subgeneric or sectional value), and he emphasized utility; Presl and Smith, using all characters, recognized a major natural group of species as a genus and emphasized naturalness. Perhaps in his day Hooker's was philosophically the sounder view, supported strongly by ex-

perience in the classification of the flowering plants. Or perhaps Presl and John Smith had an insight into the ferns that enabled them to see the limitations imposed in this particular group by the fruiting structures. In all events, for the next half-century Hooker's system dominated pteridology and prolonged the life of the Swartzian system to nearly a full 100 years. It was not effectively opposed until nearly the 20th century.

Probably the most elaborate 'Genera Filicum' was written by Antoine Laurent Apollinaire Fée (1850–52). Fée followed the Preslian school but used an even greater variety of characters. He recognized 181 genera with an additional seven of doubtful status. The fine lithographs of J. A. Villemin present details of the venation, sorus, indusium, indument, sporangium and spores. In addition to vegetative characters, Fée sought to find new characters in the fruiting structures and introduced the number of the cells of the annulus of the sporangium. Fée compared the value of this character in the ferns to that of the peristome in the classification of the mosses although subsequent study has hardly confirmed his optimism. In spite of his detailed study of this character it was not used again in a major classification until Copeland's recent 'Genera Filicum.'

Having finished his 'Species Filicum' in 1864, Hooker commenced a synoptical handbook of the species of ferns in order to place the more important information of his previous publication before the public in a more convenient form. His 'Synopsis Filicum' was completed after his death by John Gilbert Baker (Hooker & Baker, 1865–1868). The treatment of genera is almost identical to that of the 'Species Filicum' and it remained the same in the second edition of 1874. The importance of the 'Synopsis Filicum' is that it was the first handbook of ferns since that of Swartz in 1806, and its great utility was a very important factor in carrying to general acceptance the Hookerian System. Such a synopsis of species was never published by the followers of Presl.

Although John Smith was preceded by Presl in laying the foundations of the modern system, he fully established his own position by his later publication, the 'Historia Filicum' (Smith, 1875). This publication not only presented his own matured views but also integrated the numerous genera of Presl and Fée. He recognized 212 genera of Filicales, three times as many as the 'Synopsis Filicum' of 1874. Smith was the founder and curator of the living fern collection at Kew and under his care it became one of the most notable ever assembled. He had an intimate knowledge of his plants, and this is reflected strongly in his classification. Smith's views, however well founded upon observation of the living plant, were nevertheless largely ignored until the twentieth century.

The first breach in the dominance of the Hookerian system was made by Hermann Christ (1897), and it was effectively widened by Ludwig Diels in his treatment in the 'Natürlichen Pflanzenfamilien' (1898–1900). Although Christ recognized only 92 genera he did emphasize vegetative characters for genera and this basis was enlarged upon by Diels. The latter author recognized 130 genera (including Sadebeck's treatment of Hymenophyllaceae). Diels thus had almost twice as many genera as the 'Synopsis Filicum'. He gave new impetus to classifica-

tion, particularly phyletic classification which was in its initial stages. Diels attempted a phyletic presentation based on characters of the sorus and indusium. Such a basis has not actually been discredited, but in general it has been slighted by the present emphasis upon vegetative characters.

The work of Diels also stands as a landmark for the modern usage of the family as a formal category. Previous authors rarely used the family category; the major groups of genera or tribes were usually called orders or suborders. Robert Brown (1810) recognized some of the essential differences of the sporangia that were to form the primary characters for the fern families. Carl Frederick Phillip de Martius (1828–1834) listed seven major groups of his Filices, and they generally correspond closely to our modern families in form of name, characters and content but he did not designate their category. A year later (Martius, 1835) he changed this classification somewhat, recognizing five orders of ferns and under the order Filices he had seven families. These groups are without description and by comparison with the classification of the angiosperms it is clear that his category order corresponded to our modern family. Georg Mettenius (1856) brought previous usage even closer to our own, with the exception that again he used the category order for the equivalent of our family. The sporangial characters and content of his orders are very similar to those of the families of Diels. As an indication of the instability in the use of the higher categories it may be noted that while Martius had families as subdivisions of his orders, Mettenius reversed this and divided the family Filices into eight orders. Christ (1897) had major groups very similar to those of Diels but did not designate their rank. Thus although the characters of the annulus and capsule had rather early been established, our families in their modern sense and usage begin with Diels.

There was a period of great activity during the next two decades in which new genera were described and old ones revived, and, perhaps of more importance, a basis of fact was laid for a real phyletic system of classification. The studies of Karl Eberhard Ritter von Goebel, summarized in his 'Organographie' (1898–1901, 1918) and of F. O. Bower (1894–1904, 1910–1923) on the growth, development, anatomy and morphology of the fern plant, and particularly those of Sir Albert Charles Seward (1900, 1910) and Dukinfield Henry Scott (1908) on fossil ferns made a phyletic classification possible. At least, with such a broad basis of comparison, certain relations could be fairly well deduced, although others remained as largely speculative.

The first really phyletic classification was by Frederick Orpen Bower (1923–1928) who developed his phylogeny on a broad basis of anatomical, morphological, and developmental characters. He recognized twelve families of Filicales and six lines of evolution in the Polypodiaceae. Primarily due to the consideration of the difference between the marginal and superficial sorus as fundamental, these lines within the Polypodiaceae were treated as three quite independent developments. This proposal of polyphylesis for the traditional fern family is the most striking and most debated aspect of his treatment. Bower's elaborate three-volume work

is the best documented account of fern phylogeny. However, his interests were not in formal taxonomy and although he recognized separate groups of the Polypodiaceae he did not propose a system to accommodate them.

Edwin Bingham Copeland (1929) was the first systematist to deal with the problem of recognizing the polyphyletic origin of the Polypodiaceae in a formal classification. He points out that there are two alternatives, (1), to raise each phyletic line to the rank of family, or (2), define the Polypodiaceae so as to include the older types and make it monophyletic. He considers neither as free of objection but adopted the latter course. His Polypodiaceae includes the Plagiogyriaceae, Cyatheaceae, Dicksoniaceae, Matoniaceae and Dipteridaceae of Bower. Such a group, according to Bower's views, however, would not be monophyletic. A unique feature of Copeland's treatment is his interesting system of numbering the genera in such a manner as to show their place in the phyletic tree or bush. This or a similar system might be considered as a possible means of circumventing the difficulty of expressing phylogeny in a necessarily linear presentation of the genera in book form.

Carl Christensen (1938) published the first complete taxonomic synopsis that took into account the modern advances. He recognized twelve families of Filicales and about 230 genera which were based on a wide variety of characters. He divided the Polypodiaceae into fifteen subfamilies although he states in the text that perhaps it would be better to treat them as families. Within each family or subfamily the genera are arranged in a generally phyletic sequence. In considering the subfamilies Christensen agrees with Copeland, and disagrees with Bower in stating (loc. cit., p. 534): "They are not very closely related to each other but probably separate branches from an ancient common stock. . . ." As a matter of opinion and of convenience he does not include the closely related families within the Polypodiaceae, as Copeland did, but rather defines the family on the basis of the sporangium.

Three recent studies have added new views on the phyletic classification of the fern families. Ren-Chang Ching (1940) divided the Polypodiaceae into 32 families which were grouped into seven distinct lines of evolution. In general, these are the same lines that Copeland later recognized as families. Ching's work is poorly, if at all, documented in so far as justification of his recognition of the numerous families is concerned. It can hardly be given serious consideration unless we are quite ready to reject the present usage of the family category. Frederick Garrett Dickason (1946) inclines to question the full validity of many of Bower's tenets, and in particular he points out possible weaknesses in the derivation of the polypodiaceous sporangium from several different sources and the derivation of the marginal and superficial Polypodiaceae from similar marginal and superficial Simplices. Dickason accepts the numerous families of Ching but implies that the main groups of families arose more or less simultaneously from a common basic plexus. Richard Eric Holttum (1947) also attacks the validity of certain of Bower's expressed relationships and presents a revised classification of

the Polypodiaceae. He recognizes five families, the largest, Dennstaedtiaceae, containing eleven subfamilies. This family, although natural, he admits as undefinable. Especially notable in Holttum's work is the use of characters of the type of cutting and branching pattern of the leaf and also of his essentially complete denial of the basic difference of the superficial and the marginal sorus, genera of both kinds being placed in the same family.

The latest phyletic classification is by Copeland (1947) who now essentially accepts the polyphylesis of the Polypodiaceae as envisioned by Bower. He recognizes three major independent lines and classifies these in eight families. Eleven additional families of Filicales bring the total to nineteen. He has 299 genera based on a wide variety of characters and these correspond in principle, as do those of Christensen, to the genera of Presl, Fée and John Smith. In adopting separate families for the lines of evolution of the Polypodiaceae Copeland has lost definition of his groups. In fact, he freely admits Pteridaceae and Aspidiaceae as natural but undefinable. This is a consequence of his philosophical principle that a family or genus must be natural and only secondarily should be convenient. This treatment brings to the fore, perhaps more forcibly than ever before, the conflict between naturalness and utility in classification.

The next major system will necessarily be most concerned with two issues. One is the phylogeny of the Polypodiaceae, *sens. lat.*, involving primarily the nature and origin of the sporangium and the phyletic relation between marginal and superficial sori. The other is the conflict between utility and naturalness mentioned above. The first issue must still be worked out since it cannot be now considered that the phylogeny of the Polypodiaceae is sufficiently known. As to the second issue, it is now evident, at least in the ferns, that a single classification cannot have a maximum of both utility and naturalness. Bower has expressed what is probably an accurate estimate of the relation of the two types of classification (Bower, 1928, vol. 3, p. 39):

> "A complete artificial classification is always possible and is indeed necessary for floristic use. A complete phyletic classification will only become possible with complete knowledge of the descent of the organisms classified. The second cannot replace the first under present conditions, owing to the imperfection of present knowledge. But it can lead to a correction and amendment of classification for floristic use, so as to make it run ever more nearly along lines of probable evolution."

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A STUDY OF THE ARBORESCENT LYCOPODS OF SOUTHEASTERN KANSAS

CHARLES J. FELIX[1]

Studies of the anatomy of North American species of *Lepidodendron* have been largely restricted to a few recently described species. These are *L. novalbaniense* (Read, '36) and *L. boylensis* (Read and Campbell, '39), *L. Johnsonii* (Arnold, '40), *L. scleroticum* (Pannell, '42), and *L. hallii* and *L. wilsonii* (Evers, '51). *L. vasculare* has been reported by Graham ('35) and others, but this well-known European species has not been studied in detail. *L. Johnsonii* and *L. scleroticum* represent the best examples of critical studies of this genus by American workers.

The present study is based on several scores of *Lepidodendron* specimens collected from the open pit of the Pittsburg and Midway Coal Company located four miles south of West Mineral, Kansas. The abundance of these arborescent lycopod stems indicates that they were a dominant element in the Pennsylvanian flora of that area. The diversity of branch orders represented is far greater than in any other coal ball deposit that we have yet encountered, and consequently the identification of the species has been made with considerable difficulty. For reasons which are pointed out below, three distinct species appear to be represented.

LEPIDODENDRON **kansanum** Felix, sp. nov.

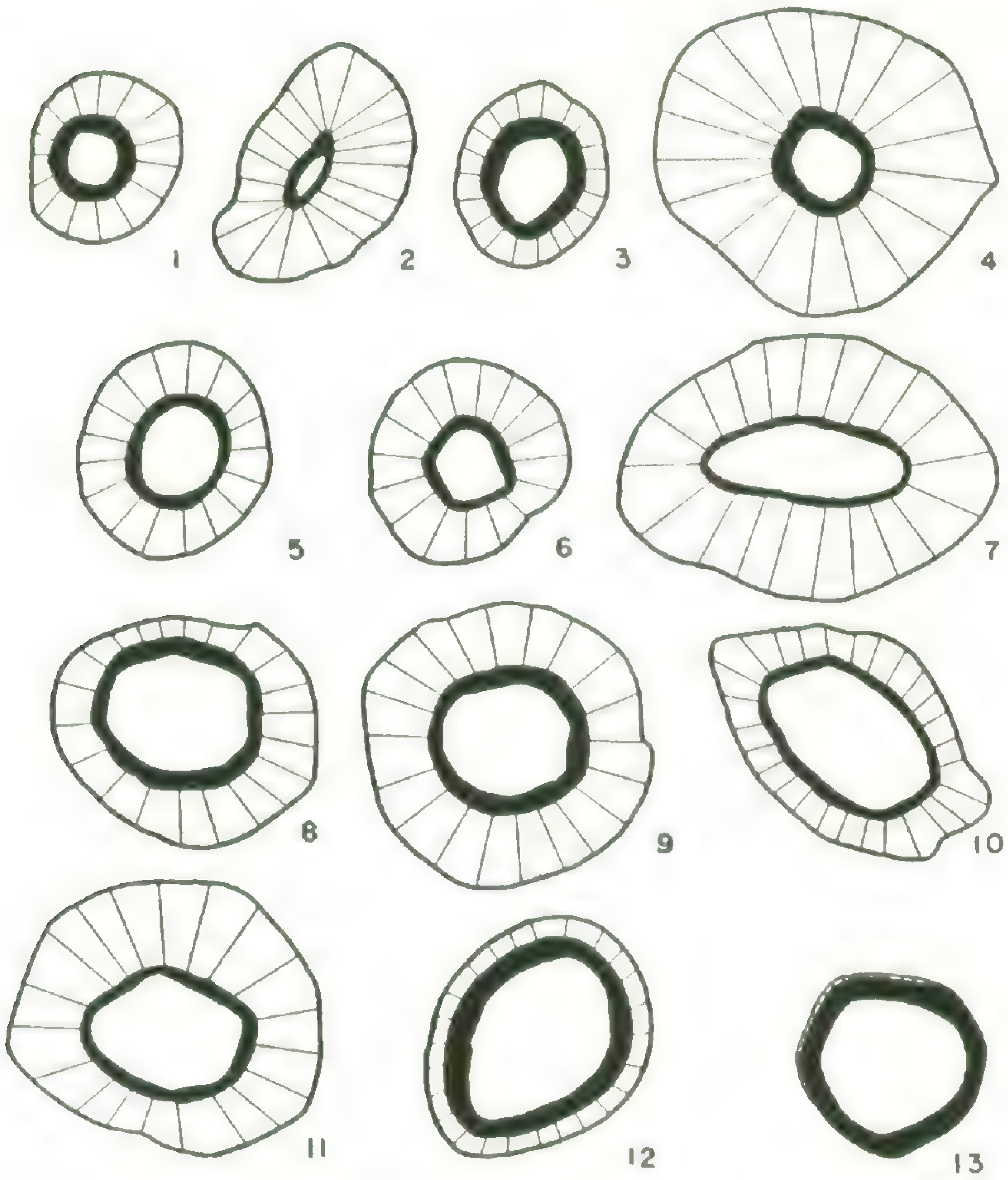
The description of *L. kansanum* is based on about twenty of the better-preserved stems although several dozen others were found which supplemented the study. While the most striking feature of *L. kansanum* is the large size of the central cylinder, there is great variation in the ratio of the diameter of the primary body to the thickness of the primary and secondary wood. Text-figs. 1–13 and figs. 5 and 6 (pl. 25) show this variation in several of the best-preserved specimens. Table I gives the dimensional relationships of the steles used in the description.

All the specimens are siphonostelic, the diameter of the pith ranging from 10 mm. (text-fig. 1) to 40 mm. (text-fig. 13). Of particular interest is the primary body-secondary wood ratios. For example, the stele shown in text-fig. 1 has a pith 10 mm. in diameter with a conspicuous (16 mm. thick) development of secondary wood, while that shown in text-fig. 13 has a pith 40 mm. in diameter, great thickness of primary wood, and but little secondary xylem. The extra vascular tissues are frequently lacking or poorly preserved in these large specimens, but as much as 63 mm. of periderm and cortical tissue are found accompanying one large stele of 73 mm. in diameter.

The Pith.—

A pith is present in every specimen and measures from 10 to 40 mm. in diameter, with excellent preservation in several steles. It consists of thin-walled cells arranged in longitudinal series; the end walls are transverse although an occasional specimen was observed in which they were irregular as if division were still occur-

[1]Graduate Assistant, Henry Shaw School of Botany of Washington University, St. Louis.



Diagrammatic transverse sections of the steles of several well-preserved plants of *L. kansanum.* Solid black represents primary xylem; radiating lines, secondary xylem; and central area, pith.

Fig. 1, WCB 772; fig. 2, WCB 706; fig. 3, WCB 778; fig. 4, WCB 821; fig. 5, WCB 761; fig. 6, WCB 767; fig. 7, WCB 776; fig. 8, WCB 771; fig. 9, WCB 765; fig. 10, WCB 800; fig. 11, WCB 769; fig. 12, WCB 704; fig. 13, WCB 824. × ¼.

ring at the time of deposition. However, these apparent divisions were not seen frequently enough to warrant a division of the pith into more than one zone such as occurs in *L. Johnsonii.* There is no evidence of tracheidal cells in the pith, the transition to the xylem being abrupt. The pith cells are nearly isodiametric and measure 162–296 μ in diameter and 133–355 μ in length.

The Primary Xylem.—

The apices of the corona are the longitudinal projections of the protoxylem (pl. 25, fig. 1) and are about 700 μ apart around the periphery of the primary stele. The course followed by the protoxylem ridges has been the subject of some debate. Seward ('10) stated that they formed vertical bands, but earlier Bertrand had described the arrangement as a lattice work. Arnold ('40) dealt at some length on the course of the ridges. It appeared to him that they divided at intervals of several centimeters, at which space the traces departed. Then from the point of division the ridges continued a parallel course as reparatory strands. Unfortunately, he was handicapped in his determination by poor preservation in the contact zone of primary and secondary wood.

TABLE I
DIMENSIONAL RELATIONSHIPS BETWEEN THE PITH, PRIMARY XYLEM, AND SECONDARY XYLEM IN THE VARIOUS STELES

Stem No.	Diameter of pith (mm.)	Diameter of primary stele (mm.)	Total diameter of stele (mm.)	Width of X_1 (mm.)	Width of X_2 (mm.)
772	10.0	19.5	51.5	4.75	16.0
706	12.0	18.0	66.0	3.0	24.0
778	17.5	27.0	43.0	4.75	8.0
821	20.0	28.0	92.0	4.0	32.0
761	24.0	29.0	63.0	2.5	17.0
767	24.0	29.0	61.0	2.5	16.0
776	28.0	32.0	76.0	2.0	22.0
771	33.0	42.5	75.5	4.75	16.5
765	34.0	44.0	85.0	5.0	20.5
800	34.0	42.0	62.0	4.0	10.0
769	35.0	40.0	80.0	2.5	20.0
704	39.0	49.5	68.0	5.25	6.0
824	40.0	50.0	50.970	5.0	0.970

In tangential sections of *L. kansanum* as many as four adjacent protoxylem ridges have been traced for a distance of 33 mm., during which space they maintain a parallel, vertical course without division or joining (fig. 23). However, other sections have revealed occasional division of the strands, and in one instance the definite departure of a leaf trace from this point of division has been confirmed.

The protoxylem cells are small, with spiral and reticulate wall thickenings. The metaxylem cells increase in size toward the center, attaining a maximum diameter of 300 μ. They average 22 mm. in length with tapered ends, although occasional cells have been measured up to 31 mm.

Both primary and secondary tracheid walls present the distinctive "Williamson's striations" observed previously in several species. There are several interpretations of their morphology, and Pannell ('42) has treated these in detail. Additional evidence that these threads are secondary in origin has been offered recently by Wesley and Kuyper ('51), who have examined the tracheids of *L. vasculare* with the aid of an electron microscope.

The Intraxylary Zone.—

The primary xylem cylinder is separated from the secondary xylem by a layer of thin-walled parenchyma-like cells with delicate reticulate thickenings of the cell walls (fig. 23). The sculpturing is not truly scalariform, and the bars average about 2.7 μ in width. These cells often form a solid layer about the primary xylem. In wall sculpture they greatly resemble the ray cells of the secondary xylem of *Lepidodendron* but appear to be smaller and more nearly isodiametric. They range from 18 to 85 μ in length and from 14 to 45 μ in width. This zone of cells is probably of common occurrence, and Arnold ('40) noted such a layer of poorly preserved parenchymatous cells in *L. Johnsonii*. Seward ('10) observed similar cells between the primary and secondary xylem of *L. vasculare*, and he noted that

such isodiametric elements are a characteristic feature of the boundary between primary and secondary wood in lepidodendroid stems.

The Secondary Xylem.—

Most of the specimens studied produced a sheath of secondary xylem around the primary cylinder; however, this sheath varied in thickness from less than a millimeter to as great as 32 mm. As in other fossil lycopods, the amount was small in comparison with the size of the stem and evidently served as a secondary factor in the support of the trunk.

The first-formed secondary tracheids are from 40 to 50 μ in width. One row of these small, first-formed secondary xylem cells is separated from the adjacent row for a short distance from the primary cylinder by narrow rows of the small reticulate intraxylary cells. The secondary tracheids gradually increase in size for about 20 cells, after which they average about 185 μ, with the largest attaining 203 μ in width. The largest, however, are much smaller than the huge metaxylem cells. The length was more difficult to determine than that of the primary tracheids; several were followed for more than 15 mm. without their limits being determined.

The xylem rays are 1 to 10 cells in height and seldom over one cell in width. In size and wall sculpturing they resemble the small cells of the contact zone between the two xylem layers.

In one specimen an unusual differentiation of the secondary xylem suggests growth rings (fig. 2), two of them being present. These rings are uniform and apparently the result of climatic changes.

The numerous leaf traces have a spiral arrangement and depart from the periphery of the primary xylem, but, as previously stated, there is no definite evidence that they originated from the corona points. They depart at a very acute angle (fig. 25), climb about 3.0 mm., and then assume a horizontal course through the entire secondary wood. In the innermost xylem the traces are very narrow and for a short distance are surrounded by the small reticulate cells of the xylem contact zone. They quickly assume a compact oval shape equal to about the width of two tracheids.

The Periderm.—

Many of the specimens possess a thick periderm; steles exceeding 8 cm. in diameter display as much as 51 mm. of periderm, although the innermost part is usually poorly preserved. The leaf bases and associated phellem are generally lacking, and the periderm is split radially into large segments, giving the outer surface a fissured appearance. However, in some specimens, sufficient periderm remains to confirm that even the largest steles were *Lepidodendron.* The periderm is quite uniform and without the concentric series of gaps which have been described in *L. vasculare* and more recently in *L. scleroticum.*

In a transverse section the cells are essentially isodiametric but with radial walls that are much thicker than the tangential walls. A similar wall thickening

has been noted in *L. Johnsonii,* and Walton ('35) called attention to it in *Lepidophloios Wünschianus.* The radial and tangential dimensions of the cells are 35–60 μ and 35–75 μ respectively.

The lumen of many cells appears to contain a brownish substance which gives the periderm a resinous appearance (fig. 3). When viewed radially, it presents a storied structure (figs. 3, 4). It is also evident that the cells are divided by lateral septa with an occasional vertical division (fig. 7). These thick-walled, chambered cells appear to be similar to those described by Kisch ('13) in unidentified specimens of *Lepidodendron* and *Lepidophloios,* and by Arnold ('40) in *L. Johnsonii.* But whereas in *L. Johnsonii* the cells are in radially placed rows of 12–30 or more in the innermost phelloderm, in *L. kansanum* the entire preserved periderm consists of chambered cells. Also, the cells of *L. kansanum* are not tangentially widened as in those of *L. Johnsonii.* They are irregularly arranged with tapered ends and are 10–15 times as long as they are wide.

Resinous substances have been reported in the periderm cells of several species. The presence of this substance probably accounts for the preservation of this tissue while the innermost periderm is usually in an advanced stage of decomposition.

Discussion.—

Walton's ('35) study of *Lepidophloios Wünschianus* from the Lower Carboniferous of Arran, Scotland, is probably the most complete structural study of a fossil lycopod. The basal portion of the central cylinder of this tree was found broken into several pieces within the hollow trunk. Walton's findings help to explain the above-mentioned lack of uniformity of the central cylinder of *L. kansanum.*

Walton was able to arrange his steles in a series which showed a transition from a small primary, solid stele 2 mm. in diameter to a large medullated cylinder of 26.5 mm. His findings clearly indicate that the basal portion of the tree consisted of a solid xylem core, which became medullated above. *L. kansanum* gives good support for such a structural explanation. Here, the smallest pith cylinder also has the smallest primary stele and a large width of secondary xylem. The specimen possessing the largest pith cylinder has the largest primary stele, but the secondary xylem is almost lacking. The secondary xylem about this largest primary stele varies from none on one side to a maximum width of 970 μ on the other. This early irregularity in the production of the secondary wood has been noted in several other fossil lycopods. Our specimens do not display as complete a transition from the smallest primary stele to the largest primary stele as is shown in *Lepidophloios Wünschianus.* However, Walton's specimen represents a single tree, whereas the specimens of *L. kansanum* were collected over an area of several square miles and are from many different trees.

It is quite probable that the specimens of *L. kansanum* do not include the basal portion of the trees. Walton's tree ranged from a solid, basal core of 2 mm. diameter to a medullated cylinder of 26.5 mm. diameter, but the diameter of the smallest primary stele of *L. kansanum* is 19.5 mm. and that of the largest is 50

mm., no protostelic specimens having been found. Other evidence that the basal portions of *L. kansanum* are not represented is suggested by the complete absence of *Stigmaria*, the basal organ of *Lepidodendron*, although several score coal balls were examined.

The structure of *L. kansanum* appears to conform to the size and form principle of Bower ('30). In dealing with the different types of steles found in the lycopods, Bower concluded that the primitive xylem column in fossil species could undergo one or more of four types of progressive changes, any one of which would have the effect of increasing the proportion of surface to bulk of the dead tracheidal tissue. These changes were: 1, fluting of the surface; 2, medullation; 3, cambial increase, with medullary rays; 4, segregation of the primary xylem into distinct strands. Medullation and cambial increase are present here, and fluting, as demonstrated by the corona, is conspicuous.

Table I presents a compilation of the dimensions of several accurately reconstructed steles. Concerning medullation, Bower stated that the formation of pith in the fossil lycopods has a general relation to the size of the primary xylem column but that the relation is not an exact one. He stated further that medullation brings with it an increased exposure of the dead tracheids to living cells, though this would not be as important functionally as increased exposure on the outer surface. In these specimens, the pith size does bear a relationship to the primary cylinder alone rather than to the entire woody stele. Text-figs. 1–13 show the increase in the primary stele to be somewhat proportional to the increase of the pith.

That the giant lycopods failed to survive perhaps indicates that they failed to maintain a sufficient proportion of presentation surface of dead wood to living cells, and thus the expanding primitive stem failed to meet the increasing requirements of translocation. However, to have even existed, such huge plants must have undergone some structural changes which would have maintained a proportional ratio of surface to bulk. Medullation seems to have been the chief means of stelar elaboration to prevent the tree from becoming physiologically insufficient, and despite their tracheid-like appearance the ray cells must certainly have been living cells, for they furnish the only effective means of maintaining the ratio of living to dead cells in the secondary xylem. The cells of the contact zone of the primary and secondary xylem present an added possibility of maintaining Bower's suggested ratio, particularly inasmuch as the prominent crenulations of the corona would serve to increase the surface area exposed.

Specific status is assigned to *L. kansanum*, although the absence of well-preserved external features and the possibility that only the upper tree trunks are represented leave many questions. It shows no significant departures from other large species of the genus, and there is little to distinguish it from large European species such as *L. brevifolium*. However, it differs from any previously described species of *Lepidodendron* of North America, and its great abundance in the Mineral flora is considered in giving it a specific diagnosis.

Diagnosis: Steles siphonostelic, large, with conspicuous variation in ratio of diameter of primary body and thickness of primary and secondary xylem; large pith composed of single type of thin-walled, nearly isodiametric cells; massive periderm composed of fiber-like chambered cells divided by lateral and vertical septa, uniform and not irregularly zoned by decay of less resistant cells; primary xylem limited externally by prominent corona formed by projecting exarch protoxylem elements; zone between primary xylem and secondary xylem occupied by numerous thin-walled parenchyma-like cells with reticulate wall sculpture.

Locality and Horizon: Strip mine of the Pittsburgh and Midway Coal Company, Cherokee County, Kansas; Fleming coal, Cherokee Group, Des Moines Series, middle Pennsylvanian.

Type specimens: The author is cognizant of the taxonomic problems involved in the designation of fossil types. However, the following specimens best show the characteristics of this species: WCB 706, WCB 767, WCB 770, WCB 821, and WCB 824, Washington University, St. Louis.

Lepidodendron **dicentricum** Felix, sp. nov.

The description is based on a number of small stems, but not as many as of *L. kansanum*.

The Stele.—

The primary xylem is of particular interest. It consists of an inner and an outer xylem which are sharply differentiated from each other (pl. 27, fig. 18). One small stele (WCB 781), 9.5 mm. in diameter, has an excellently preserved inner primary xylem 5 mm. in diameter. It is composed of short, barrel-shaped, nearly isodiametric tracheidal elements (pl. 26, figs. 14, 16). The cell walls are distinguished by delicate scalariform and reticulate thickenings, and "Williamson's striations" are also present. The cells range from 70 to 300 μ in length and 50–175 μ in width. A larger specimen (WCB 775), with a stele of 18.5 mm. in diameter, contains an inner primary xylem 9 mm. in diameter.

The outer primary xylem is continuous about the inner. There is no noticeable corona, but there are exarch protoxylem elements. The small protoxylem cells measure 8–25 μ in diameter, and spiral thickenings are present in the smallest cells. The larger metaxylem cells are 40–190 μ in diameter and are scalariform. The tapering tracheids average about 15 mm. in length.

A similar central cylinder is characteristic of *L. vasculare*, in which the outer edge of the primary stele consists of narrow tracheids. Toward the center the diameter of the tracheids gradually increases, and parenchymatous cells mingle with elongated scalariform elements. The central region is composed of parenchyma arranged in vertical series of short cells, interspersed with short tracheids distinguished by greater wall thickness and scalariform and reticulate thickenings.

In *L. dicentricum* there is a clear differentiation between the outer and inner primary xylem zones (fig. 13). There is no mixture of tracheids and parenchyma, all cells of the central region being tracheidal.

The origin of pith has been an important and debated problem, and the central organization of *L. dicentricum* seems worth consideration. It is generally accepted that the siphonostele developed from the protostele, either as a cortical "invasion" (Jeffrey, '10, '17), or as a modification of the central part of the protostele (Boodle, '01, and Gwynne-Vaughan, '03). The intrastelar pith origin has received its chief support from studies of lepidodendrids, *L. vasculare* being one of the better known. The central region of the pith, known as a mixed or partial pith (fig. 9), has been considered as transitional between true protosteles and true siphonosteles. The long, thick-walled tracheids with scalariform wall sculpture are mingled with long septate cells. Some of the short segments of the septate cells are thick-walled with scalariform sculpture, while others are thin-walled and without any wall thickenings, appearing parenchymatous in every respect. Thus it would seem that the pith is formed from a subdivision of tracheids into short tracheary elements, then into parenchymatous cells, and all stages may be seen in the central area of the stele of *L. vasculare*.

The primary xylem cylinder of *L. dicentricum* differs from that of *L. vasculare* in that the entire central area is homogeneous, consisting of isodiametric cells with pronounced scalariform and reticulate thickenings.

It would thus appear that this species offers clear evidence of an intrastelar origin of the pith and presents a transitional type between a protostele and siphonostele.

The parenchyma-like cells observed between the primary and secondary xylem of *L. kansanum* were evident, although generally poorer preservation rendered them more difficult to distinguish. The secondary xylem was 3 mm. in thickness in one of the better specimens. However, badly compressed material of far larger specimens was found, and the maximum dimensions probably far exceed 3 mm. The innermost tracheids of the secondary xylem are small and delicate and are from 18 to 37 μ in diameter. They enlarge gradually outwards to a diameter of 122–137 μ on the outer edge of the woody stele.

The leaf trace originated from the protoxylem cells at the periphery of the primary xylem, and, departing at an acute angle, it followed a horizontal course through the entire secondary wood. In its course through the secondary xylem the trace consists of short, scalariform cells averaging 40 μ in width and 200 μ in length. Upon leaving the secondary wood the trace follows a vertical course for several millimeters along the face of the secondary xylem (fig. 10), and in WCB 775 the trace climbed vertically for a distance of 16 mm. During this climb there is some decrease in the width of the tracheids which measure 18–33 μ. The trace follows an oblique course upward through the cortex and resumes a horizontal course through the periderm. It is more difficult to follow the leaf traces beyond the periphery of the secondary xylem, but the cortex and periderm form a network, probably due to decay of parenchymatous tissues surrounding the leaf trace, and the fragmented traces may be found in the gaps.

The Cortex.—

The cortex appears to have consisted of two zones. The inner cortex, directly adjoining the stele, is, when preserved, composed of delicate, parenchymatous cells with much thinner walls than those of the outer cortex. The well-preserved outer cortex consists of parenchymatous cells which are irregularly arranged. These cells are elongated and the ends taper slightly.

The cortical cells range from 40 to 208 μ in diameter and from 75 to 600 μ in length, with the larger and shorter cells adjacent to the xylem and the smaller and longer ones nearest the periderm. Although there is a regular decrease in cell diameter from the xylem outwards to the periderm, an intermingling of small cells throughout serves to form a large number of intercellular spaces (fig. 11).

In a tangential section the cortex presents a reticulate appearance (fig. 22). This is produced by the passage of the leaf trace and the partial breakdown of the large amounts of parenchyma cells which surround the traces. A similar cortex has been described in *L. scleroticum,* but that species was characterized by sclerotic nests of cells which are absent here.

The Periderm.—

The periderm consists of radially arranged fibrous cells with rather thick walls. In a radial section they present the uniform storied structure characteristic of *Lepidodendron,* and all cells in a series are of equal length. When viewed tangentially they show an irregular, interlocking arrangement, the cells being 640–825 μ long by 35–65 μ in radial diameter and with tapered ends.

A phellogen is occasionally visible, and many of the thin-walled cambium cells have decayed, leaving a gap between phellem and phelloderm. In WCB 775 the phellogen laid down about 130 cells to a row on the interior (phelloderm) and about 15 to the exterior (phellem), giving some idea of the ratio of these two tissues. The periderm interior to the phellogen, morphologically a phelloderm, is characterized by series of holes as if caused by decay. Various interpretations have been given to periderms with such gaps (fig. 19). Hovelacque ('92) described them in *L. selaginoides* as less-resistant layers formed at periods of slack growth. Many authors have interpreted them as secretory organs, the most recent of these being Arnold ('40). However, the periderm of *L. dicentricum* does not show the orderly tangential arrangement of glands as in *L. Johnsonii* or *Lepidophloios Wünschianus,* nor is there any cellular structure in the gaps to suggest anything but decayed or less-resistant cellular structure. The phellem is characterized by rows of tangentially widened, thin-walled cells (fig. 20). Such rows of cells have been defined by Kisch ('13) as "meshes", and the term will be used here with the same meaning.

In a smaller specimen (WCB 817) in which no secondary xylem had formed, the periderm could be observed in its earliest stages. The mesh cells of the phellem had just begun to make their appearance, and the mesh rows were only about 5 cells in length. The phelloderm of this specimen contained about 30 cells to a row.

Kisch ('13), in a comprehensive account of the periderm, described a heterogeneous periderm. As the simplest variation from the ordinary periderm cell she figures a type which has become chambered by horizontal, and occasionally vertical, septa. The most complex type of periderm which she figures is that known as "Dictyoxylon Cortex". This consists of a network of ordinary periderm cells, while the meshes, visible alike in transverse and tangential sections, are filled with thin-walled, block-like parenchymatous cells. This complex periderm has been described in *Sigillaria spinulosa*, and Williamson ('78) noted such wedge-shaped rows of cells in unidentified lycopod bark. Renault and Grand'Eury ('75), in their work on *Sigillaria spinulosa,* found the meshes absent in the inner periderm tissue but present in the outer periderm and gradually increasing in size towards the periphery. A similar occurrence may be seen here in a transverse section where the first cells of the mesh are the size of fiber cells and widen tangentially towards the outer phellem (fig. 20).

The thin-walled, tangentially widened cells of the meshes in a tangential section of the periderm are divided by horizontal septa into chambers such as those found in the inner phellem adjacent to the phellogen (fig. 15). These cells are the same as the simple chambered ones described by Kisch ('13). Each segment then appeared to undergo further vertical divisions along with horizontal divisions until the original extended cell shape disappears (fig. 12), and only the pointed end segments leave a clue to the origin of the meshes. This sequence of cells can be followed in tangential serial sections from an inner chambered cell outward through a series of increasingly complex divisions until there remains a network of a few periderm fibers about many block-like parenchymatous cells, the latter representing the first mesh cells laid down by the phellogen (text-fig. 14). The only cells of the mesh in the inner portion of the phellem are the chambered ones with a few horizontal septa. The cells of the mesh increase in size and complexity of division towards the outer phellem.

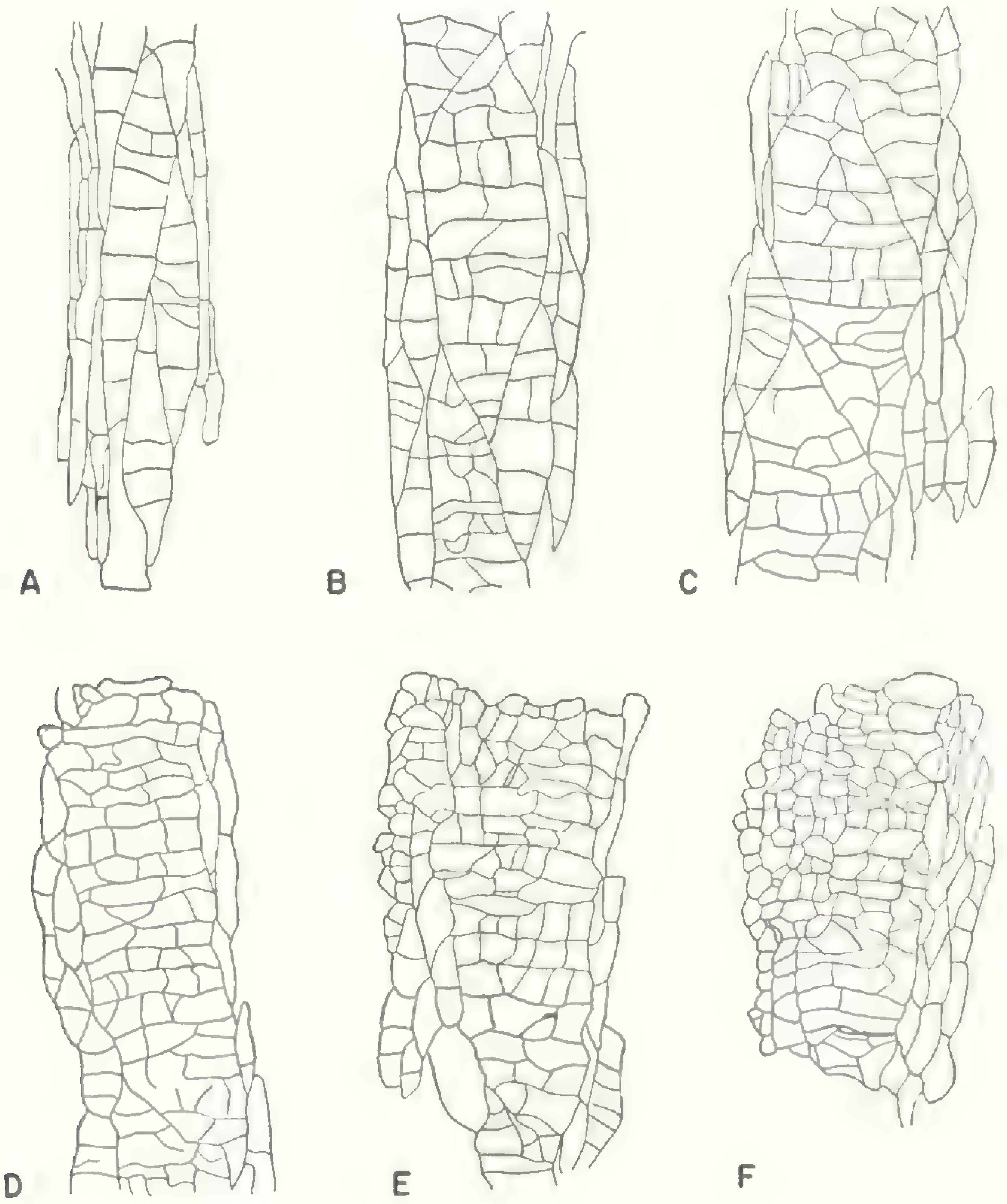
This periderm has only two cell types, the unchambered fibers of the phelloderm and the phellem, and the chambered cells restricted to the phellem. The differences in the chambered cells represent stages in the formation of the "Dictyoxylon Cortex." This "Dictyoxylon Cortex" is not to be confused with the primary outer cortex of *Lyginopteris* and *Heterangium* with its strands of fibrous sclerenchyma, to which the same term is applied.

The Parichnos.—

A surface view of a leaf base of *L. dicentricum* reveals two parichnos strands, one on either side of the leaf trace. They are reniform in shape and average about 0.6 mm. by 0.3 mm. A groove about 1.8 mm. long runs across the leaf cushion beneath the strands (fig. 8). In some species, notably *L. aculeatum* and *L. sternbergi,* two oblong marks appear below the parichnos strands, one on either side of the median line. Weiss ('07) made a detailed study of such scars, which he called lateral pits, and he found that the parichnos strand joined up with two

patches of specialized cells close below the leaf scar. He described a group of delicate stellate cells joining the parichnos to the specialized cell group, and he termed these as aerenchyma. Hovelacque ('92) also described an opening beneath the parichnos, but it was a single pit-like depression similar to the one in *L. dicentricum.* He illustrated it in his paper on *L. selaginoides* and gave it the name "sillon inférieur". However, he did not mention any connection between the depression and the parichnos strands.

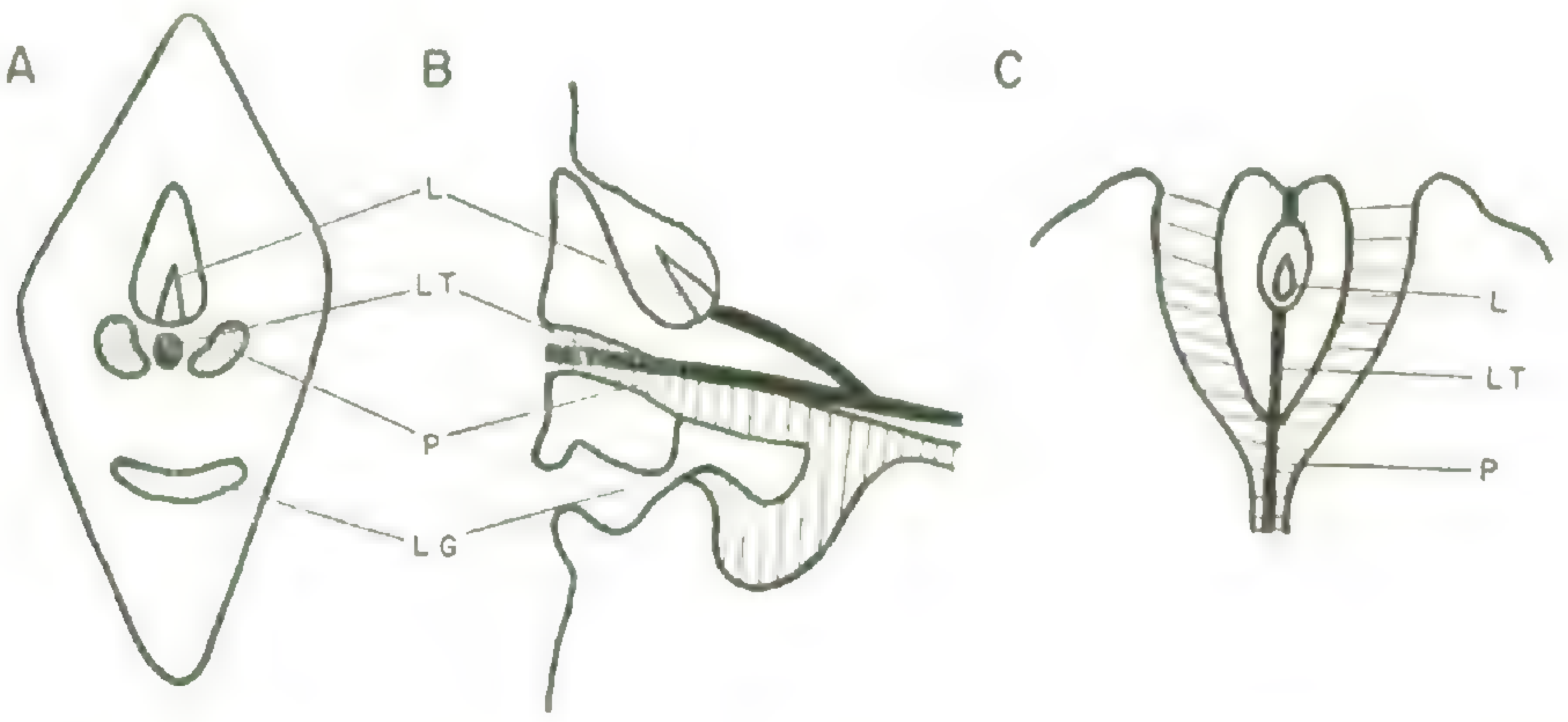
Due to faulty preservation, it has been difficult to determine the actual point where the parichnos makes its appearance. It is first observed, however, in the middle of the cortical tissue. Tangential sections of the tissue reveal large gaps which give the cortex a reticulate appearance. The gaps contain fragments of



Text-fig. 14. Camera-lucida drawings of mesh of *L. dicentricum* in tangential section of outer periderm. × 31.

A. Approx. two cells or 68 μ from the phellogen; B. Approx. seven cells or 306 μ from the phellogen; C. Approx. eleven cells or 476 μ from the phellogen; D. Approx. sixteen cells or 680 μ from the phellogen; E. Approx. twenty-one cells or 850 μ from the phellogen; F. The outer limits of the mesh approx. 1 mm. from the phellogen.

leaf-trace xylem accompanied by a large band of thin-walled parenchyma cells resembling those of the outer parichnos strands. The gaps can be followed through the thick-walled outer cortex and through the periderm where they continue to form a network as a result of partial decay of the parenchyma cells. These thin-walled cells completely surround the leaf trace on its journey, but the bulk of the tissue lies below the trace.



Text-fig. 15. Diagrammatic views of a leaf cushion of *L. dicentricum:* L, ligule; LT, leaf trace; P, parichnos; LG, lateral groove.

A, tangential section; B, longitudinal section; C, transverse section.

In transverse sections the parichnos strands can be seen leaving the periderm horizontally and bifurcating in the leaf base at the outermost edge of the periderm. The two strands diverge right and left of the vascular bundle, and, passing obliquely upwards, they assume positions on either side of the trace (text-fig. 15). In a longitudinal view the strands are seen to join a body of parenchymatous tissue below the point of bifurcation, and as they pass upwards they come near to the leaf-cushion surface below the trace scar. This body of tissue is exposed to the outer surface by an open groove (fig. 21). This groove corresponds to the lateral groove seen in face view (fig. 8) and to the "sillon inférieur" of Hovelacque.

Weiss ('07) worked out in detail in several species the relation of the parichnos to the scars below the leaf cushion. He showed some parichnos strands which bend downwards before leaving the cushion as in *L. Veltheimianum.* Others pursued a straight, gradually ascending course but below the leaf scar contacted a specialized aerenchymatous tissue which is exposed on the depressions below the leaf scar. In *L. dicentricum* there is a downward bending of the parichnos at the point of division resulting in the large nests of parenchymatous tissue. As the tissue appears identical to the remainder of the parichnos, it seems of little importance whether it is a downward bending of the strands or a nest of tissue. It is important, however, that here is another addition to a more efficient aerating system for these large plants. That this is a group of specialized cells such as Weiss described is entirely possible, for there is usually a small area of decayed cellular structure between the mass of cells and the main parichnos strand, and this corresponds to the position of his delicate stellate cells.

The Ligule.—

A ligule pit about 1 mm. deep is located on the upper surface of the leaf cushion immediately above the leaf trace scar. About 0.5 mm. of the ligule is usually visible, inserted obliquely at the base of the deep flask-shaped cavity (fig. 21), but it is too imperfectly preserved to reveal cellular structure. The base of the cavity lies above the leaf trace, and a strand of short tracheids forms a connection between the ligule cavity and the leaf trace. The tracheids to the ligule have delicate scalariform thickenings and range from 88 to 168 μ in length and 20 to 40 μ in width. This vascular connection of the ligule to the trace is of some interest in that neither Seward ('10), Scott ('20), nor Hirmer ('27), in their excellent surveys of *Lepidodendron,* note it. Emberger ('44) diagrammed such a connection, but perhaps the most authentic evidence has been reported by Evers ('51). He noted its presence in *L. hallii* with transfusion tissue extending from the leaf trace upward to the base of the ligule pit. A similar connection has also been reported as occurring in *L. Hickii.*

Discussion.—

An earlier reference has been made to the resemblance between *L. dicentricum* and *L. vasculare,* and it is felt that for clarification a further comparison of the two is warranted. *L. vasculare* has been treated with great detail by Seward ('10), and the excellent plates of Hovelacque ('92) and his detailed account of the anatomy leave this fossil as one of the best described.

The outer periderm of *L. dicentricum* is characterized by the rows of tangentially widened mesh cells; such cells have never been figured for *L. vasculare.*

The cortical tissue differs greatly. The inner cortex of *L. vasculare* usually disappeared at an early stage. The outer cortex consisted of two types of tissue: isodiametric cells alternated with radially arranged areas of tangentially elongated cells which extended as wedges into the inner phelloderm. In larger stems the phelloderm is characterized by its tapered form (fig. 17) as a result of decay of the elongated cortex cells. The isodiametric cells persisted. The outer cortex of *L. dicentricum* is a single cell type, and no cortical tissue extends into the phelloderm.

There are other differences of a more minor nature. The secondary xylem of *L. vasculare* usually assumes a cylindrical form of unequal width about the primary xylem (fig. 9); that of *L. dicentricum* is laid down uniformly. While the periderm of *L. dicentricum* does show series of holes, these do not appear to be the same as the regular concentric rows of apparent secretory strands in the phelloderm of *L. vasculare.*

Diagnosis: Exarch primary cylinder without prominent corona; primary xylem of two zones, an inner one of short, nearly isodiametric thick-walled cells with scalariform and reticulate thickenings, and an outer zone of elongate scalariform tracheids; secondary xylem usually present but frequently lacking in smaller stems; outer cortex of thick-walled elongated cells which decrease in diameter and increase

in length toward periderm; thick periderm irregularly zoned from apparent decay of less resistant cells, inner periderm (phelloderm) composed of radial rows of fibrous cells of secondary origin, outer periderm (phellem) characterized by rows of fibrous cells and rows of thin-walled, tangentially widened cells of cambial origin; a lateral groove present in the face of the leaf cushion beneath the parichnos strands; below leaf scar region of cushion the parichnos joins a body of parenchymatous tissue which is exposed to the outer surface by opening of the lateral groove.

Locality and Horizon: Same as for *L. kansanum.*

Type specimens: WCB 775 and WCB 781, Washington University, St. Louis.

Lepidodendron **serratum** Felix, sp. nov.

Specimens of this *Lepidodendron* are quite numerous in the Kansas flora. Several excellent specimens, as well as numerous more fragmentary ones, were available for study. This description is based chiefly on the following three specimens: a slightly compressed stem 43 mm. by 16 mm. in diameter, which ran entirely through the coal ball (WCB 798) for a distance of 30 cm.; a specimen (WCB 707) showing branching (fig. 27), and an excellently preserved specimen (WCB 815) of one of the smaller stems (fig. 29). All the specimens were siphonostelic, and there was no evidence of the development of secondary xylem or of a periderm.

TABLE II

MEASUREMENTS OF VARIOUS ANATOMICAL COMPONENTS OF SPECIMENS FROM COAL BALLS 798 AND 815

	No. 798	No. 815
Stem diameter including cortex	43.0 × 16.0 mm.	8.0 × 6.0 mm.
Stele diameter	9.0 × 6.0 mm.	1.0 mm.
Pith diameter	7.5 × 2.5 mm.	0.40 mm.
Width of primary xylem	2.0 mm.	0.3 mm.
Diameter of protoxylem elements	13–26 μ	16.5–27.0 μ
Diameter of metaxylem elements	59–89 × 198–260 μ	36–79 × 56–108 μ
Diameter of pith cells	36–79 μ	16–43 μ
Length of pith cells	85.8–184.8 μ	49.5–125.4 μ

Table II illustrates the weakness in designating species on the basis of measurements of anatomical components as is occasionally done. There is no doubt that these specimens belong to the same species, but the difference in size of the anatomical components is conspicuous.

Peels made of tangential stem sections of *L. serratum* show a characteristic shape of leaf bases (fig. 28). When viewed tangentially, the margins of the typical cushions appear wavy or serrate. The radial view is equally distinctive (fig. 24), and the cushion tapers off basally in a series of prominent protuberances which extend down the narrow groove separating the cushions (figs. 24, 30). Frequently the emergences are seen to run from the cushion base to the next cushion in the spiral. In WCB 815 the emergences projected from 225 to 400 μ

and even more in the larger stems. They are epidermal in origin (fig. 30) and possess no vascular tissue. The stem of *L. serratum,* with the exception of the upper portion of the leaf cushions, is clothed with the emergences, and certainly these tiny projections must have presented a distinctive appearance.

A ligule is situated in a pit near the apex of the cushion (fig. 26), and the vascular trace enters the leaf beneath the ligule. The trace is accompanied by the parichnos strand. The parichnos does not fuse with any parenchymatous tissue in the lower leaf cushion as in *L. dicentricum,* and no lateral groove is present in the face of the leaf cushion.

The Pith.—

The pith is composed wholly of unsculptured, thin-walled cells. Their size varies, with the larger cells being found in the larger stems, but all appear to be about three times as long as broad in the species.

The Vascular Tissue.—

Exarch primary xylem only is present, no secondary wood having been observed in this species. It forms a band which varies from 0.3 to 2 mm. in width in the different specimens. The largest metaxylem tracheids, which are adjacent to the pith, measure over 200 μ in diameter, and the smaller tracheids of the protoxylem measure 13–27 μ in diameter. The scalariform tracheids of all the xylem elements show "Williamson's striations".

The mesarch leaf trace departs from the edge of the xylem, and for a few millimeters it climbs almost vertically. After the trace leaves the xylem it still continues to climb at a very steep angle. In WCB 815 a trace was followed vertically for a distance of 14 mm., during which it moved 4 mm. horizontally through the cortex. The leaf trace in this species never assumes the oblique course in the cortex as is usually the case in *Lepidodendron;* rather it climbs almost vertically from its initial appearance until it enters the leaf base. A similar trace is characteristic of *L. aculeatum* Seward ('06).

Several stems exhibiting branching were found, most of them being less than 10 mm. in diameter. The branching was usually monopodial, a stem being shown in fig. 27 with two branches departing. It appears that they departed at different levels, for the branch the greatest distance from the main axis has nearly regained its normal circular form, while the one nearest the main axis still retains its crescent shape.

The Cortex.—

Directly adjoining the xylem is an area of imperfectly preserved tissue about 1 mm. in width. A band of compact parenchyma composed of small block-like cells abuts on this zone of disintegrated tissue. Two other clearly defined zones of tissue succeed this band, and a similar organization has been described in other species of *Lepidodendron.* Seward ('06) pointed out anatomical characters of *L. aculeatum* quite comparable to those of *L. serratum.* Seward termed the band of compact parenchyma the inner cortex and the succeeding zones as middle and outer cortex; the same designations are used in this description.

The inner cortex measures 0.37 mm. to 1 mm. in width in the different specimens. It is a very compact tissue of small, nearly isodiametric cells 16–46 μ in diameter and 29–100 μ in length, being about twice as long as wide. The boundary between the inner and middle cortex is quite definite due to the junction of the vertical rows of the small, blocky cells of the former with the loosely organized large, irregular cells of the latter, which tend to increase horizontally rather than vertically. The middle cortex is often badly disorganized, leaving the inner cortex as a ring about the xylem cylinder.

The cells at the inner edge of the outer cortex are short and rather flat, and in longitudinal sections they exhibit a fairly regular vertical arrangement. However, they gradually assume a more elongated form toward the outer stem surface and range in length from 39 μ at the innermost to 215 μ at the outermost edge.

The cortical organization of *L. serratum* bears a close resemblance to *L. aculeatum*. However, the external characters of the latter are greatly different from those of *L. serratum*. Seward ('10) discussed the resemblance which his *L. aculeatum* showed to *L. fuliginosum*, a species for which specimens have been described with external characteristics of *Lepidodendron* and *Lepidophloios*. It appears quite evident that the same anatomical characteristics may be associated with more than one specific form of stem as defined by the form of the leaf cushions.

The Ligule.—

The ligule pit has a narrow orifice which opens into a flask-shaped structure within the leaf cushion (fig. 26). The pit is set at a very acute angle and is approximately 1 mm. deep. The ligule itself is frequently well preserved in these specimens, and in WCB 815 several ligules were present, occupying the enlarged basal portion of the pit cavity. The preserved ligule was usually about 330 μ long and varied in width from 130 μ at its base to 85 μ at the distal end. The cellular structure is composed of thin-walled parenchymatous cells. They are isodiametric and measure 15–20 μ in diameter. There is no evidence of vascular tissue between the ligule and the leaf trace as occurred in *L. dicentricum*.

Discussion.—

The pith of *Lepidodendron* might well serve as an aid in identification of species. In *L. kansanum* the pith cells were nearly isodiametric, and Evers ('51) found the same to be true in *L. wilsonii*. However, Evers reported that the pith cells of *L. hallii* were six times as long as broad. In *L. serratum* they are three times as long as broad. All the specimens mentioned above possess a pith which is a single cell type, but Arnold ('40) described a pith of two distinct zones in *L. Johnsonii*.

The presence or absence of secondary wood is not a dependable specific character in *Lepidodendron*, and it is questionable as to how much importance may be attached to its absence in *L. serratum*. It does not seem unreasonable to assume that this plant had reached maturity in the larger specimens, although far smaller specimens of *Lepidodendron* are known in which secondary xylem has developed,

and smaller specimens of *L. dicentricum* occurred without secondary wood but with periderm tissue present. In WCB 820 a specimen of *L. serratum* has 14 mm. of cortical tissue without the appearance of a periderm. Frequently the worker is overly impressed by the size of the specimen, a character which is not necessarily fundamental, and there is little reason why *L. serratum* cannot represent the mature state despite its small size. Approximately twenty specimens were found, and often almost entire coal balls consisted of tangled masses of badly compressed remains of *L. serratum* associated with a varied flora. However, not a single specimen with secondary vascular or cortical development was present. Indications are that it might have been a lax, flexuose plant which branched frequently, and its lack of secondary growth would have afforded such a plant very little support.

Diagnosis: Exarch siphonostelic primary body; secondary xylem development and periderm formation lacking; leaf bases long and tapering with serrate margins; stem clothed with numerous small, epidermal emergences which occur on all plant parts except the upper leaf cushion; homogeneous pith of thin-walled cells 3 times as long as broad, no tracheid-like cells appearing in the pith; leaf trace mesarch, following a steep, almost vertical course from the xylem to the leaf base; cortex of three zones: a compact inner cortex of small, nearly isodiametric cells, a middle one of loosely organized, large, irregular cells, and an outer one of compact cells, increasing in length toward the outer periphery of the stem; branching frequent, characterized by an unequal dichotomy.

Locality and Horizon: Same as for *L. kansanum.*

Type specimens: WCB 707, WCB 798, and WCB 815, Washington University, St. Louis.

Acknowledgment.—

The author wishes to express appreciation of the guidance and constructive criticism of Dr. Henry N. Andrews, under whose direction this work was accomplished.

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Explanation of Plate 25

Lepidodendron kansanum Felix

Fig. 1. Transverse section, showing corona projections of the primary xylem. WCB 704, × 38.

Fig. 2. Transverse of outer secondary xylem, showing zone of differentiated xylem. WCB 802, × 15.

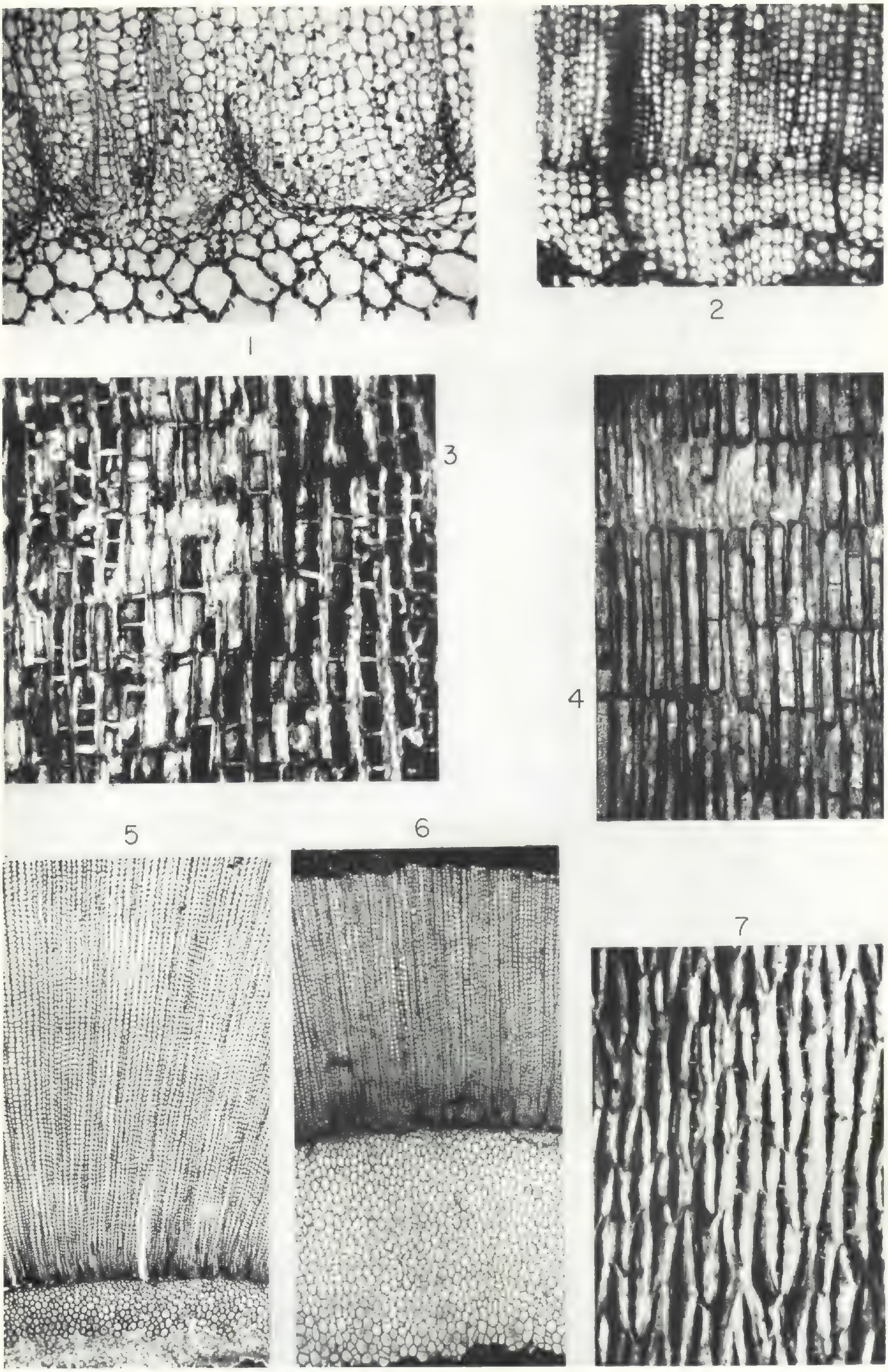
Fig. 3. Radial section of periderm, showing dark contents of the cells. WCB 770, × 35.

Fig. 4. Radial section of periderm, showing the evenly aligned cells. WCB 774, × 35.

Fig. 5. Transverse section, showing primary xylem and adjacent secondary xylem. WCB 702, × 5.

Fig. 6. Transverse section, showing primary xylem and adjacent secondary xylem. WCB 704, × 8.

Fig. 7. Tangential section of periderm, showing septate cells. WCB 770, × 38.



FELIX—ARBORESCENT LYCOPODS

Explanation of Plate 26

Lepidodendron dicentricum Felix (Except fig. 9)

Fig. 8. Tangential section, showing leaf cushion with lateral groove beneath the ligule. WCB 775, × 5.

Fig. 9. Transverse of young stele of *Lepidodendron vasculare*. × 7.

Fig. 10. Radial section through stem, showing trace departing from secondary xylem. WCB 775, × 44.

Fig. 11. Transverse section of cortex. WCB 775, × 44.

Fig. 12. Tangential section of outer phellem, showing mesh cells. WCB 775, × 45.

Fig. 13. Radial section, showing the inner primary xylem (left) and adjacent cells of the outer primary xylem (right). WCB 781, × 40.

Fig. 14. Radial section through inner primary xylem, showing wall sculpturing of cells. WCB 781, × 60.

Fig. 15. Tangential section of inner phellem, showing mesh cells. WCB 775, × 45.

Fig. 16. Transverse section through inner primary xylem, showing wall sculpturing of cells. WCB 781, × 60.

FELIX—ARBORESCENT LYCOPODS

Explanation of Plate 27

Fig. 17. Transverse of older stem of *Lepidodendron vasculare*, showing the tapered phelloderm, × 2½.

Lepidodendron dicentricum Felix

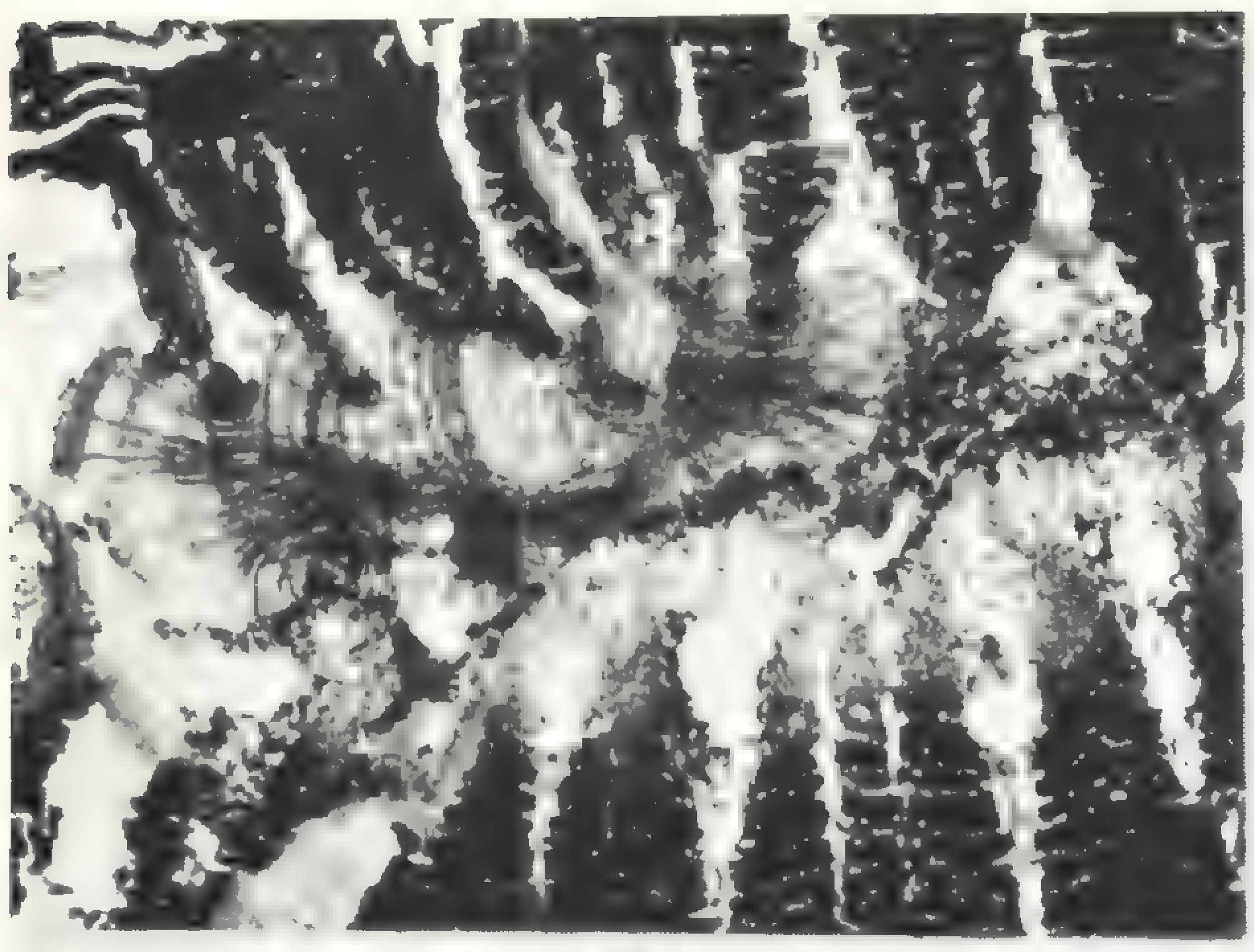
Fig. 18. Transverse of stele, showing inner and outer primary xylem with adjacent secondary xylem. WCB 781, × 7.

Fig. 19. Transverse of outer portion of stem, showing periderm. WCB 775, × 5.

Fig. 20. Transverse of phellem, showing single row of mesh cells. WCB 775, × 33.

Fig. 21. Radial section through leaf cushion: L, ligule; VT, vascular tissue; LG, lateral groove. WCB 775, × 34.

Fig. 22. Tangential section of cortex, showing reticulate appearance due to departing traces. WCB, 775, × 3½.



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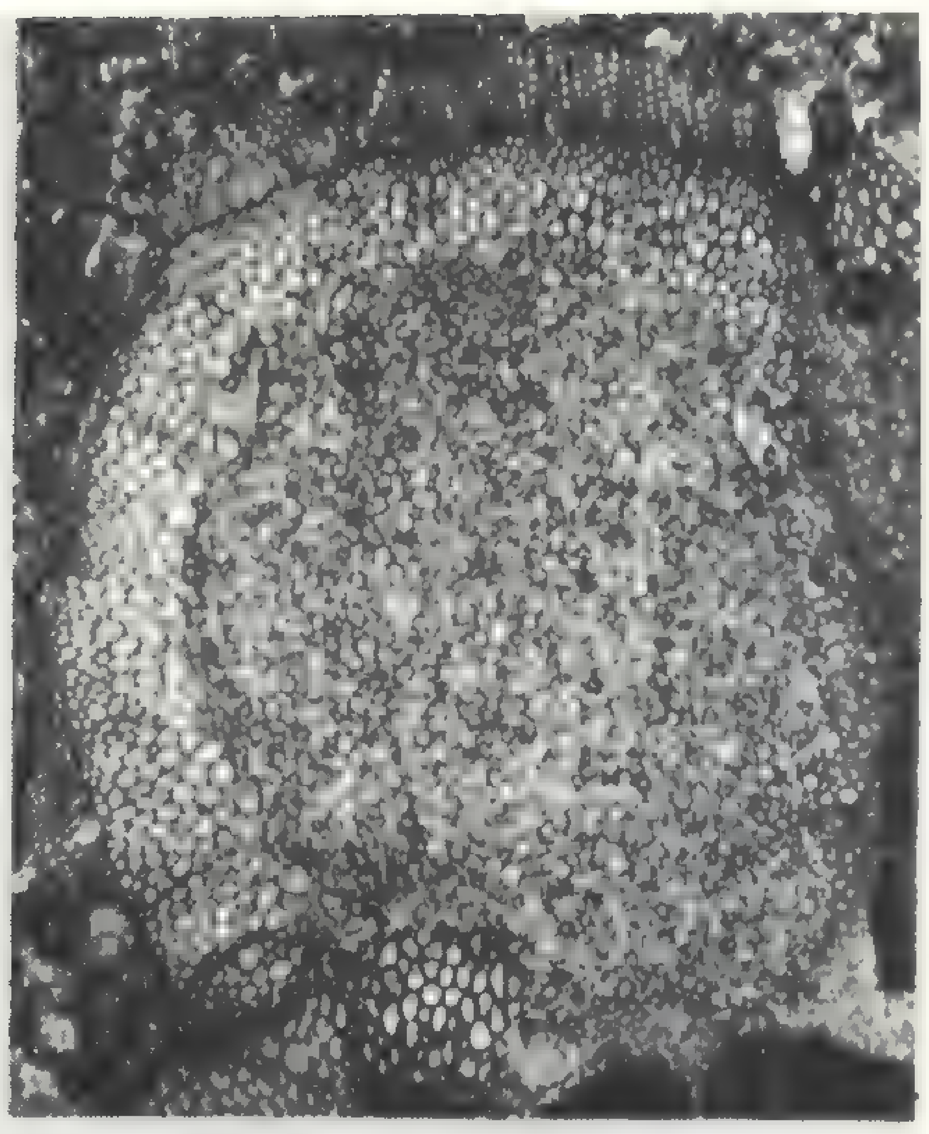

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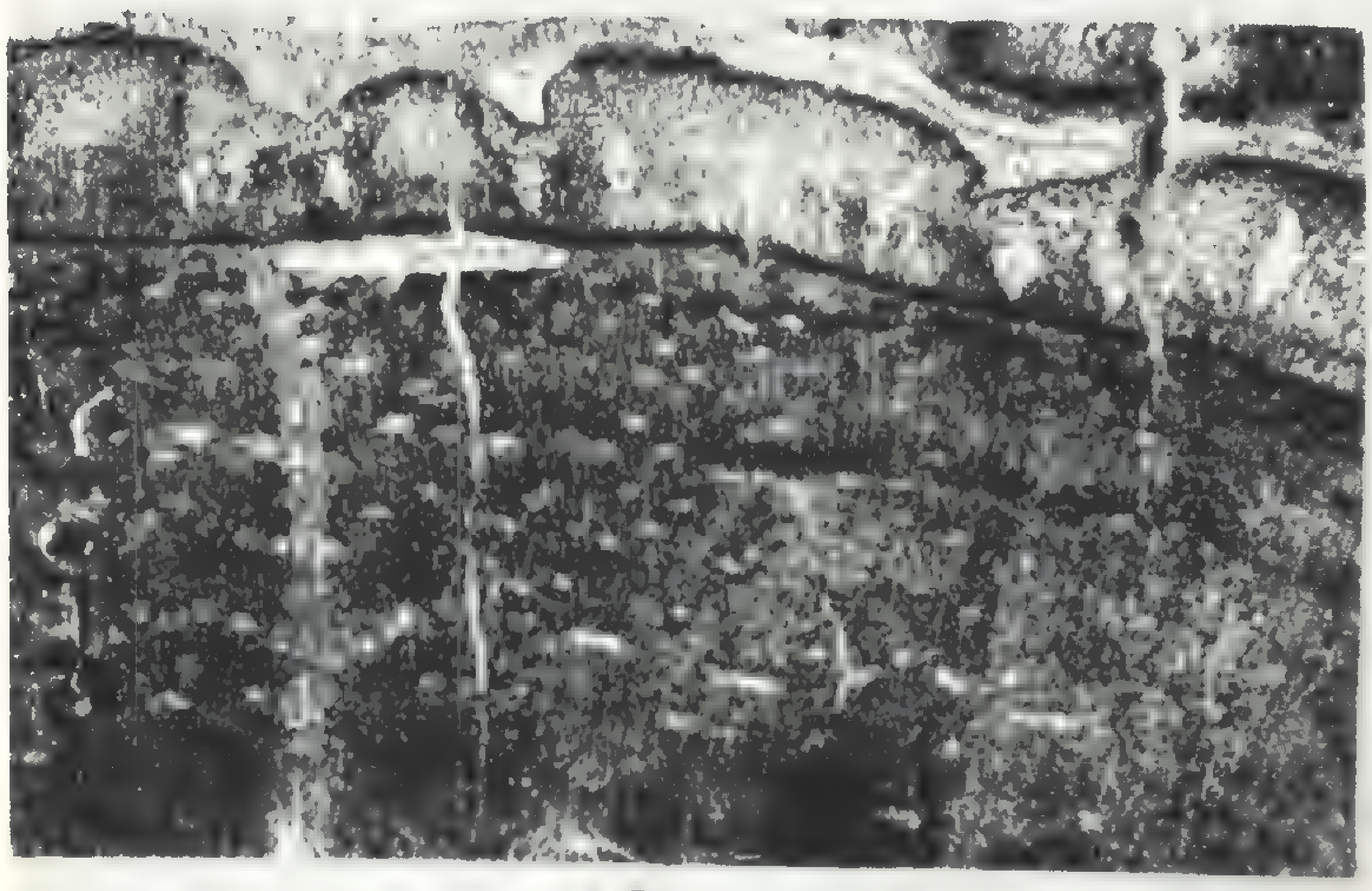

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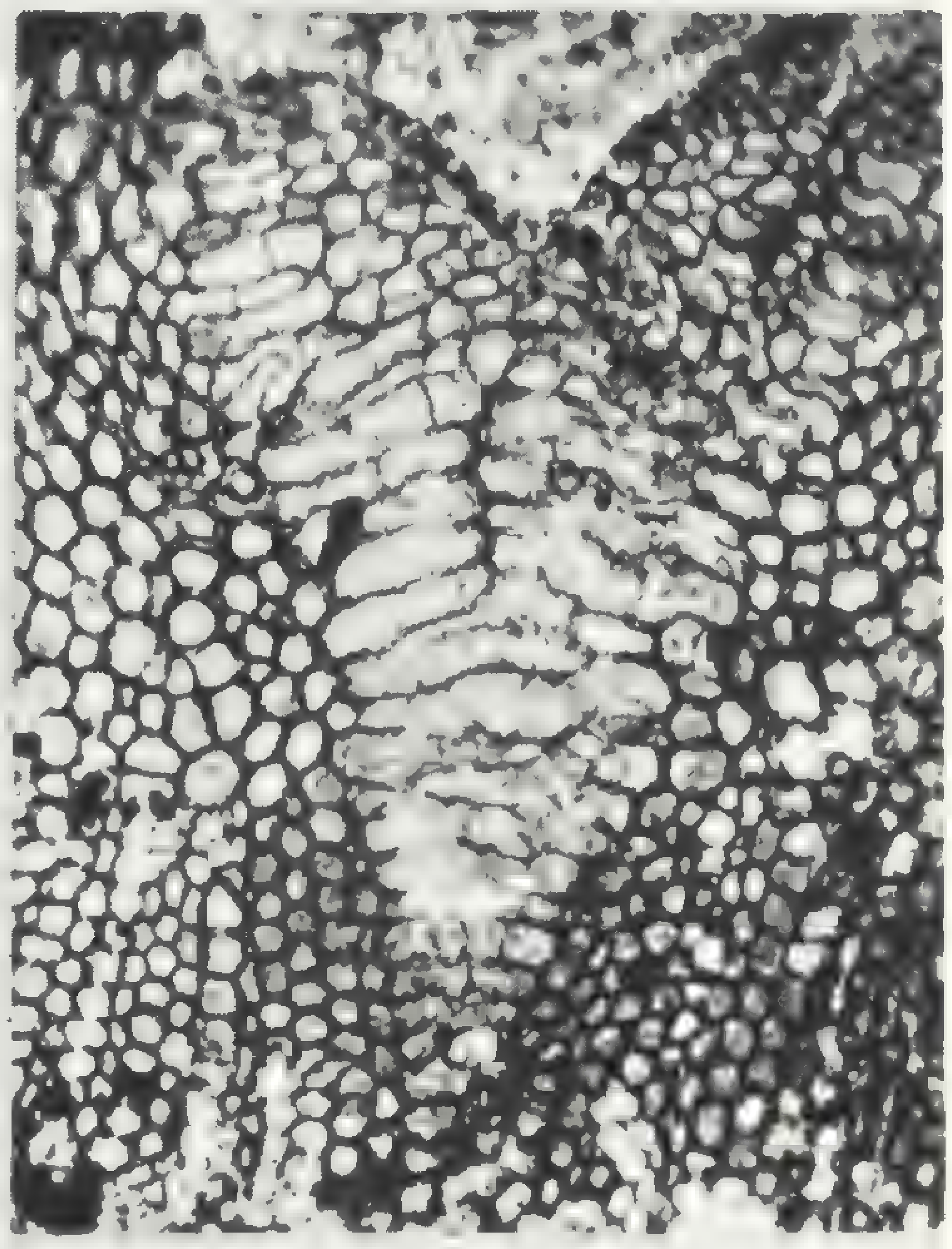

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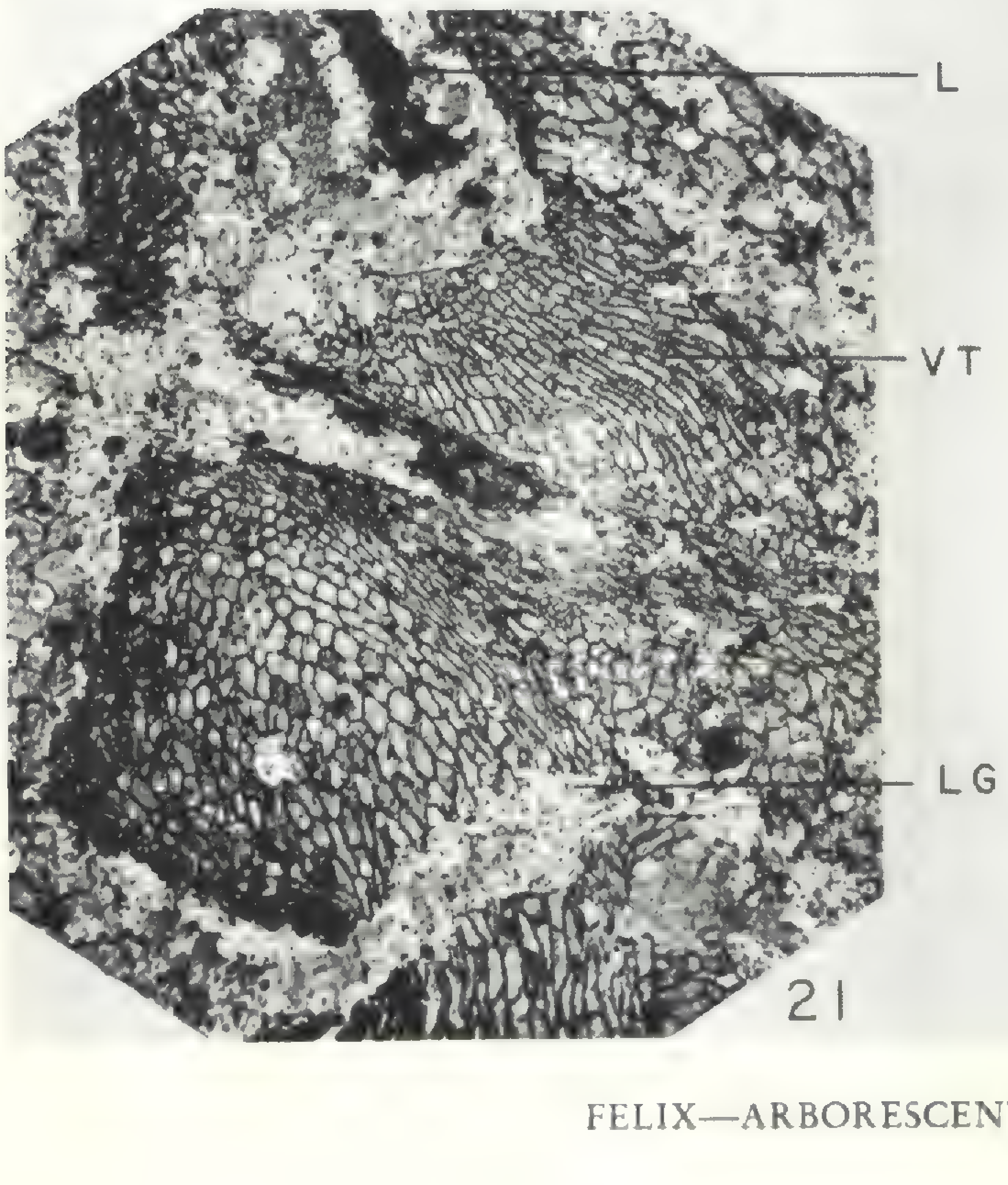

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FELIX—ARBORESCENT LYCOPODS

Explanation of Plate 28

Lepidodendron kansanum Felix

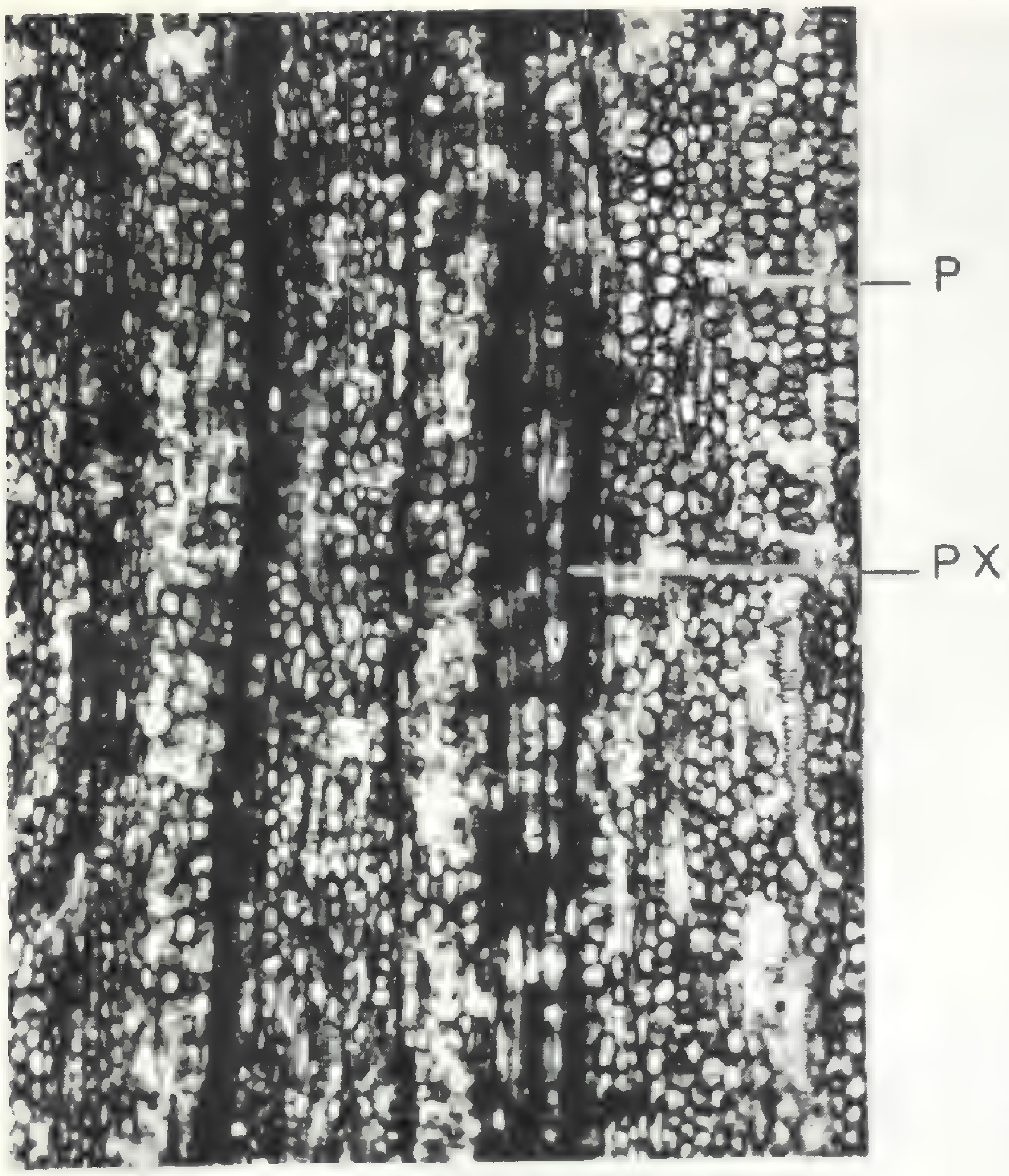
Fig. 23. Tangential section, showing zone of parenchymatous (P) cells between primary and secondary xylem. Dark strands (PX) represent the protoxylem ridges. WCB 767, × 60.

Fig. 25. Radial section, showing leaf trace departing from the primary xylem. WCB 706, × 48.

Lepidodendron serratum Felix

Fig. 24. Radial section of outer cortex, showing epidermal protuberances. WCB 815, × 28.

Fig. 26. Radial section of leaf cushion, showing ligule. WCB 815, × 54.



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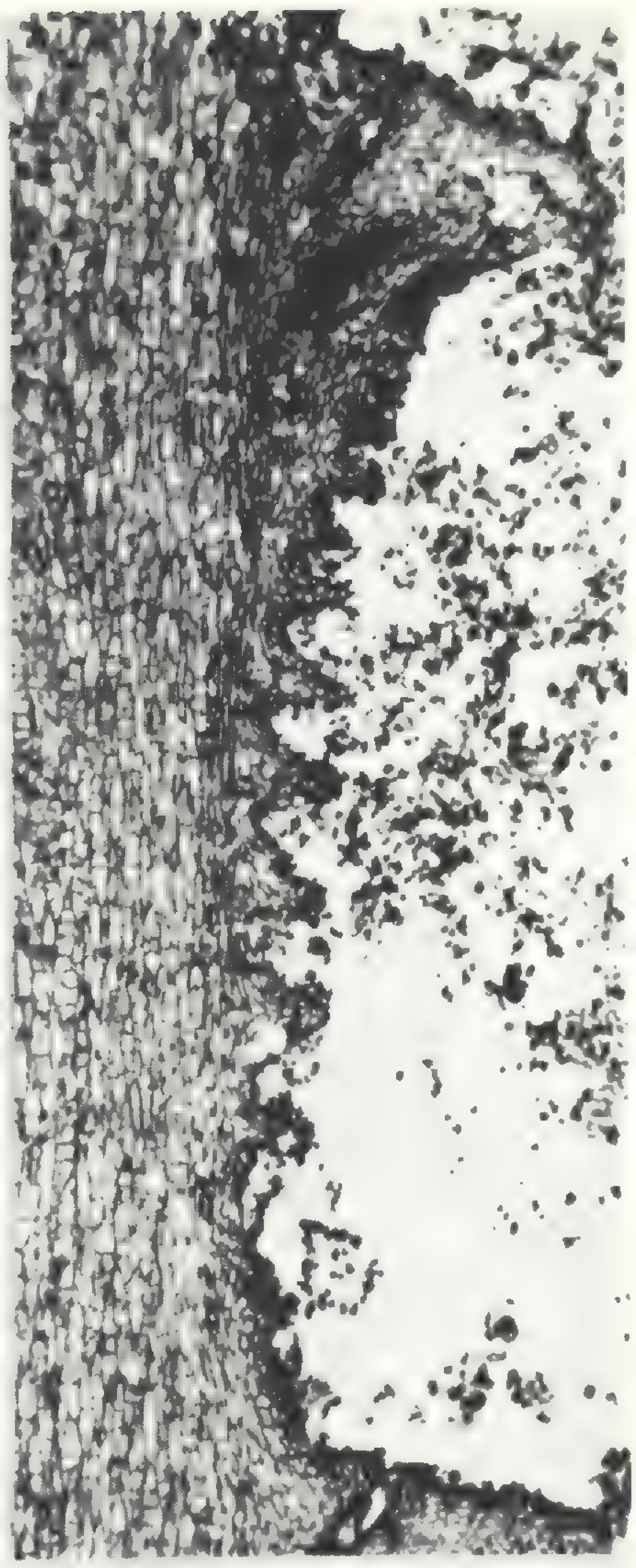

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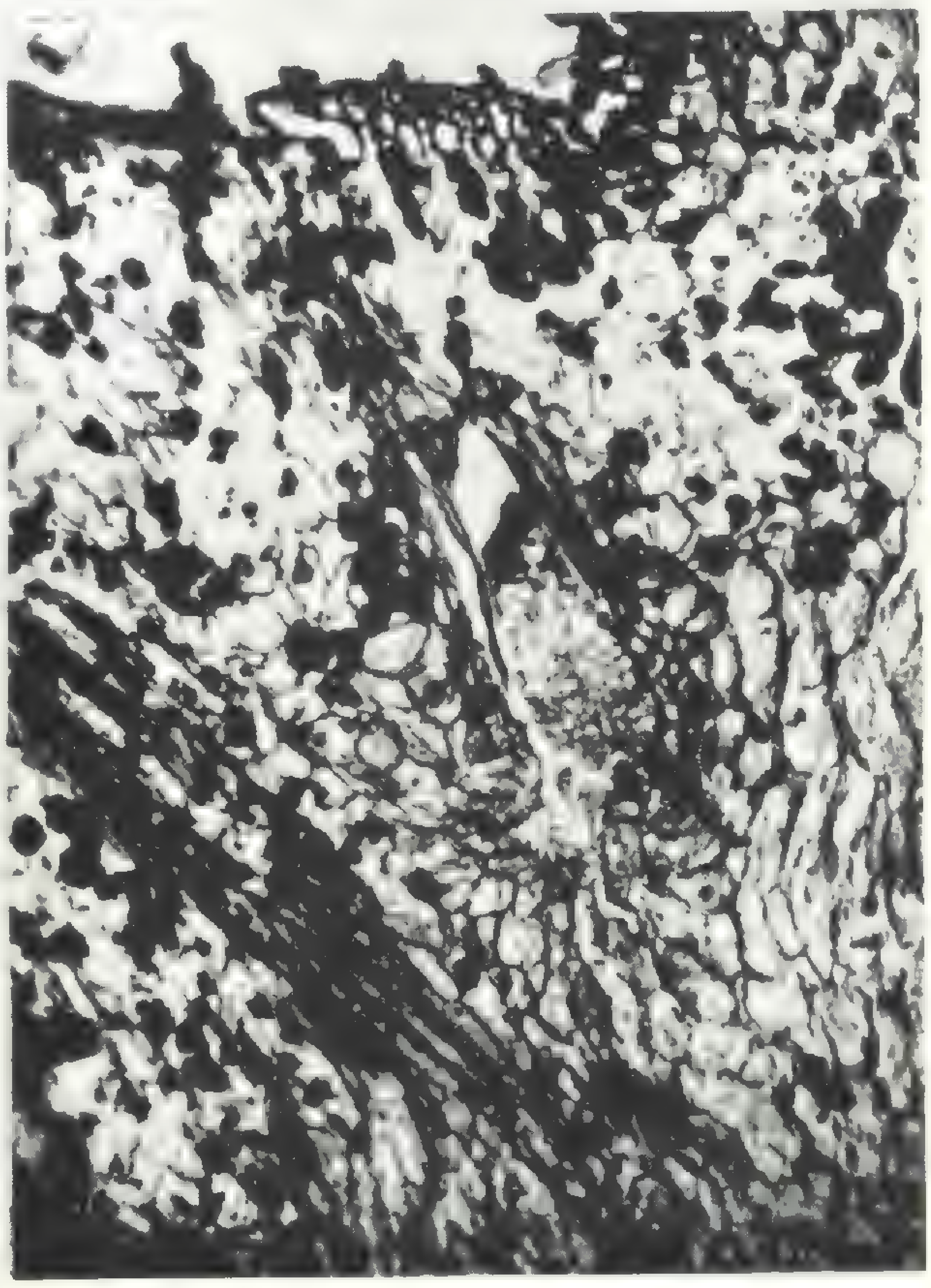

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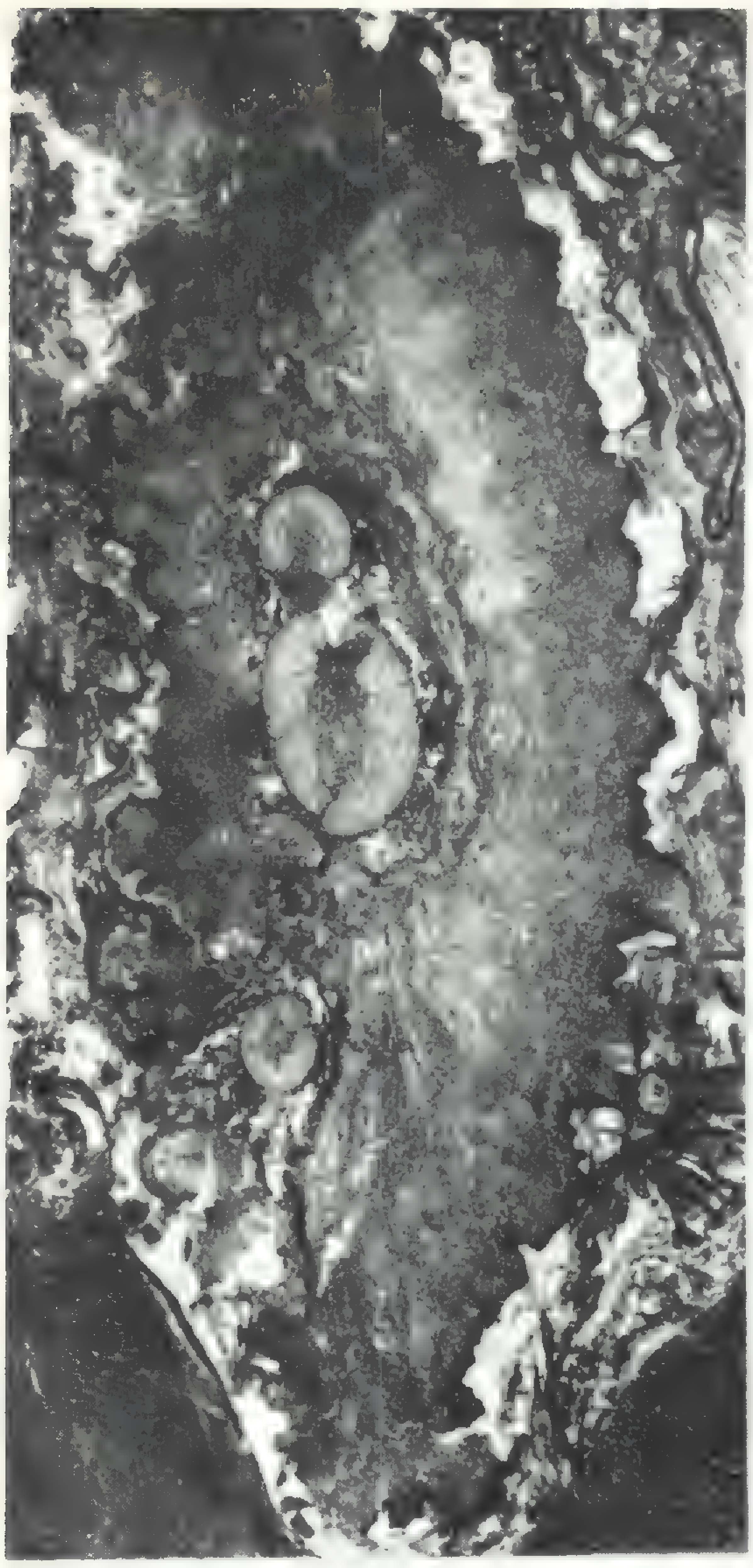
FELIX—ARBORESCENT LYCOPODS

Explanation of Plate 29

Lepidodendron serratum Felix

Fig. 27. Transverse section of stem, showing branching stele. WCB 707, × 4.
Fig. 28. Tangential section of stem, showing the leaf bases. WCB 798, × 3½.
Fig. 29. Transverse section of small stem. WCB 815, × 10.
Fig. 30. Enlarged view of epidermal protuberances. WCB 815, × 60.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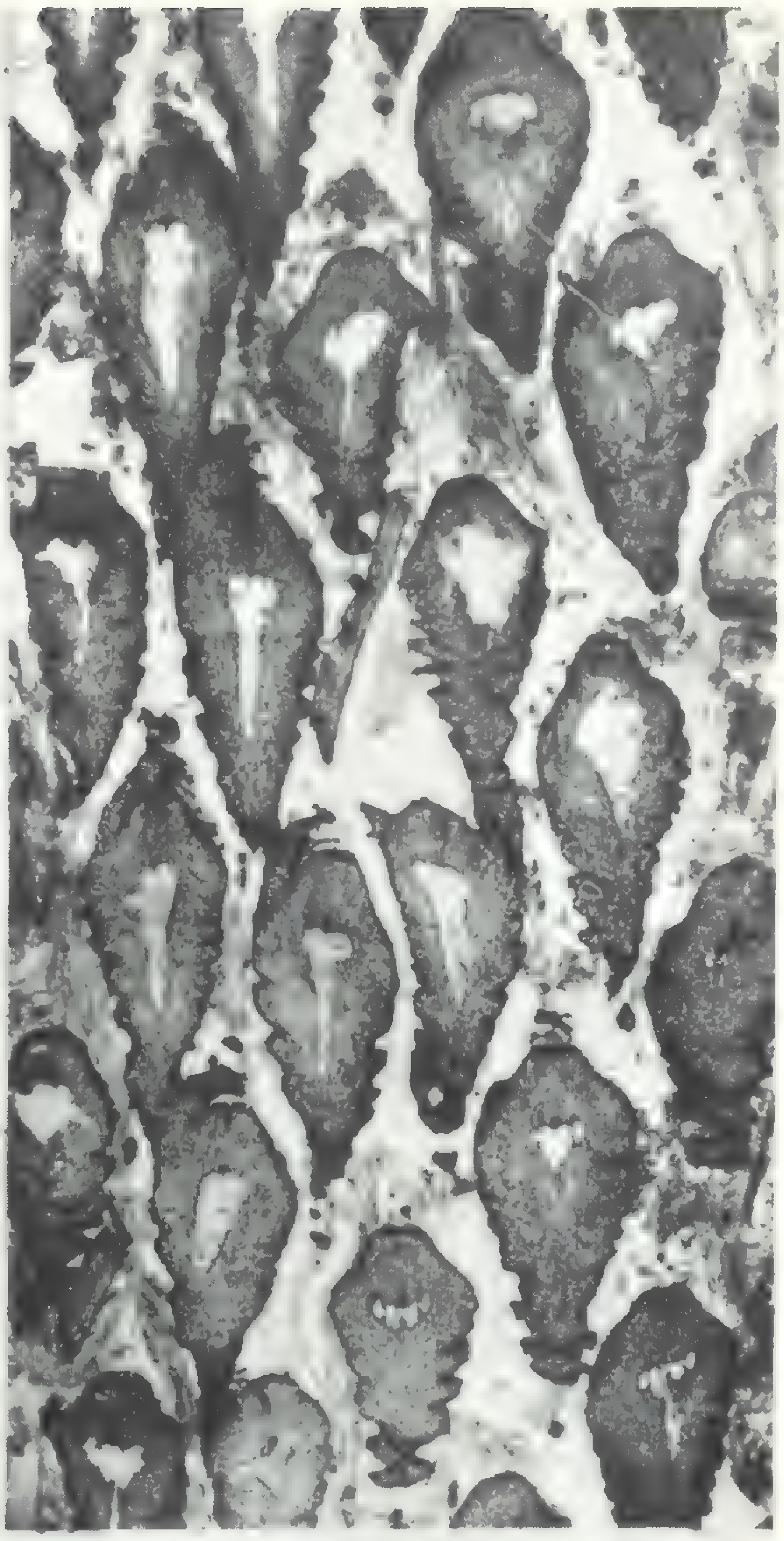
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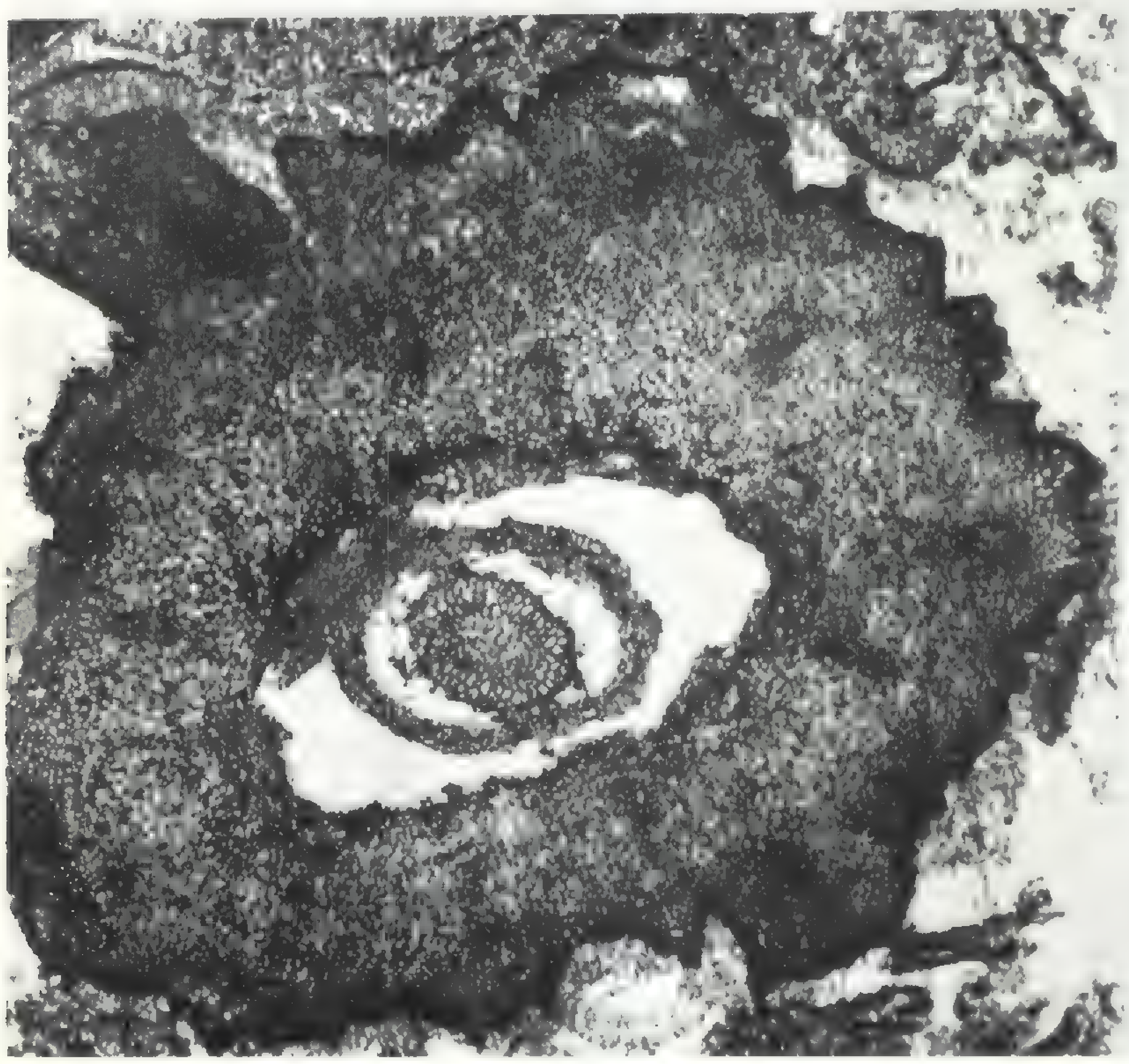

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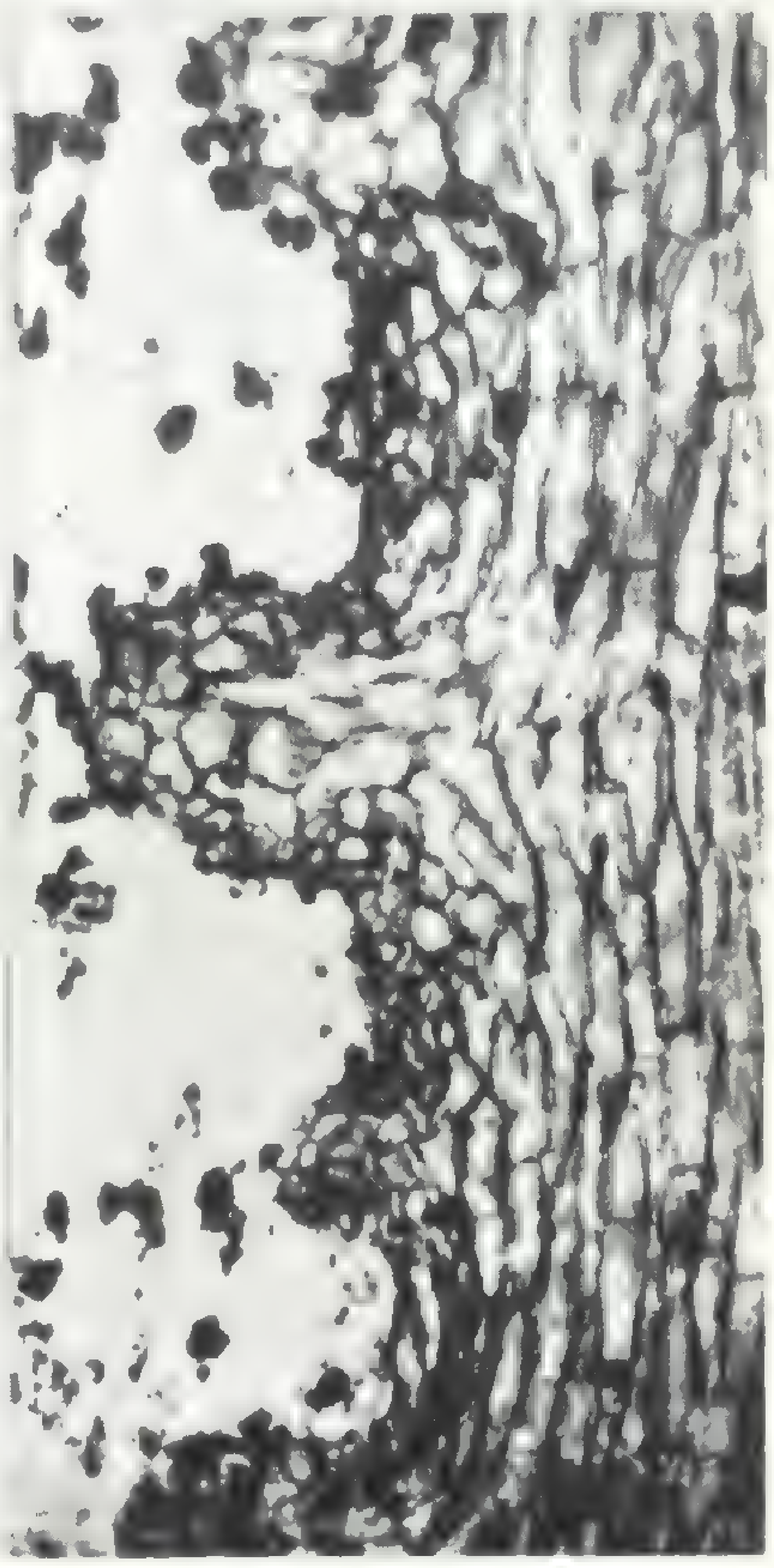

FELIX—ARBORESCENT LYCOPODS

THE HISTORY OF THE USE OF THE TOMATO: AN ANNOTATED BIBLIOGRAPHY*

GEORGE ALLEN McCUE

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Foreword by Edgar Anderson

In working out the history of a cultivated plant there are two effective avenues of approach. We may use purely botanical evidence and trace the connections between the modern crop and its original wild progenitors. We may, on the other hand, study the history and development of the ways in which a particular crop is used. With the tomato, this other kind of evidence throws a wholly new light on its history and presents us with a previously unsuspected problem: where and how did Europe get not only the tomato but an appreciation of its enormous culinary and dietary potentialities?

When McCue began his studies of the tomato it was soon apparent that the problem was a much larger one than had been supposed. He has accordingly presented his data as an annotated bibliography from which other scholars may proceed in beginning their research.

The botanical facts about the tomato are simple. It belongs to a genus of weed-like plants native to northwestern South America. By processes as yet unknown the cultivated sorts developed out of these small-fruited weeds and spread to Mexico by the time of the Conquest. The facts with regard to the history of the *use* of the tomato are far more complex. McCue's bibliography establishes the fact that our appreciation of its dietary importance is quite modern and that it came to us, not from Mexico, but by way of the Italians and the French. The bibliography also suggests (though it does not go far enough to establish definitely as a fact) that the French in turn took over the use of tomatoes from the Italians and that the Italians themselves acquired it from the Turks, or at least from peoples in the Levant.

* An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Arts in the Henry Shaw School of Botany of Washington University.

Where did the Turks become acquainted with the usefulness of the tomato? From a series of interviews made for another purpose and as yet unpublished, I can enlarge the question raised by Mr. McCue's bibliography. There is a wide and apparently coherent area in which the tomato has been used for a long time (one does not know precisely how long but it is certainly a matter of centuries) as a part of the everyday diet of everyday people. Throughout that area it is used in sauces and in meat and vegetable mixtures. Throughout that area for winter use it is dried (or half-boiled, half-dried). Throughout most of that area there are meaty varieties with relatively little juice which lend themselves well to such practices. This area now extends from southern France to Italy through the Balkans, throughout Turkey and into the edge of Iran. Towards Arabia and Ethiopia its boundaries are not so sharp and are difficult to determine for a variety of reasons.

How and when did the tomato become so closely identified with Levantine culture? This is a difficult problem but one which could eventually be solved by carefully executed research. Mr. McCue's bibliography points out one of the routes by which we can find the answer.

Introduction

There are several pieces of information which may aid the reader in his use and evaluation of this bibliography.

Initially it might be prudent to emphasize the limits of this work as indicated by the title. It seeks only to present an annotated bibliography of the history of the *use* of the tomato. Nomenclature, origin, development, etc., have been considered only in so far as they bear upon the problem of usage.

By far the major part of the titles cited are in the library collections of the Missouri Botanical Garden, including the Sturtevant Pre-Linnean collection. Smaller numbers are from the collections of the Folger Shakespeare Library, Washington, D. C.; the Library of Congress; the Library of the Department of Agriculture; and the Library of Washington University, St. Louis, Mo.

As a glance at the table of contents will reveal, the citations have been first grouped geographically. A dozen areas covering most of the world's surface were chosen with as much correspondence to historical unity (in terms of the tomato) as possible. Some serious compromises with this principle were made, however, in the interests of simplicity and workability. For example, in terms of the history of the use of the tomato, the categories of Asia and Africa are extremely heterogeneous. However, the number of references in either of the two categories is too small to give any meaning to further division. The same is true of the artificial category designated "South Pacific."

It will be noticed that there is a large area omitted from any consideration in this bibliography: neither Central America nor South America have been included.

There seems to be adequate justification for this omission. These areas are, from all evidence, the home of the tomato both wild and cultivated; its use in these areas is quite ancient. Thus, the history of the use of the tomato in most of these areas is a very different problem from the one which necessarily would be the focus for the rest of the bibliography, namely, the history of the usage of the tomato among peoples to whom it was introduced, fully developed as a food plant, in comparatively recent times. Certainly, the problem of research is very different.

Within each geographical unit there has been a further chronological division. In general the literature is covered from the first mention of the tomato in a given area until it has achieved substantial popularity in the same area A very few of the best of the modern works which touch in some way upon the history of the use of the tomato have been included under their publication dates. These are further identified in their annotations.

Whenever possible pertinent material in each work has been quoted, if in modern English, verbatim. Old English spelling has been modernized, however, and all other languages have been quoted in a close but free English translation. All translations have been identified with the abbreviation "(Tr.)." In no case have titles been translated or had their spelling modified. However, in the case of some of the older works particularly, only enough of some of the quite lengthy titles have been quoted to identify the work unmistakably.

Frequently a single work will contain references to the use of the tomato in several countries or to several different periods in the same country. Such references are quoted in their entirety only once and cross references are made. In the case of several older works which appeared in several editions, published in different countries and different languages, the complete annotation appears either in the country and under the date of the earliest edition or under the date of the first English edition. In these cases cross references have been made. Agnes Arber's 'Herbals'[1] has been used as an authority for much of the information concerning the older works (1544–1670).

Acknowledgments.—I should like to acknowledge my deep indebtedness to Dr. Edgar Anderson for his inspiration and guidance; to the members of the library staff of the Missouri Botanical Garden, for encouragement and assistance above and beyond the call of duty; to Dr. Louis B. Wright and the trustees of the Folger Shakespeare Library for the financial aid which enabled me to visit and work at the Folger Library and other libraries in the Washington area; and to Dr. Wright and the staff of the Folger Library for their kindness and help during that visit.

ITALY

1544—Matthiolus, Petrus Andreas. Di Pedacio Dioscoride Anazarbeo libri cinque della historia, et materia medicinale trodotti in lingua volgare Italiana. Venetia, 1544.

[1] Arber, Agnes. Herbals, Their Origin and Evolution. New edition. University Press. Cambridge, 1938.

p. 326. In a chapter on the mandrake *(Mandragora)* the following description of the tomato occurs: "Another species [of Mandrake] has been brought to Italy in our time, flattened like the melerose [sort of apple] and segmented, green at first and when ripe of a golden color, which is eaten in the same manner [as the eggplant—fried in oil with salt and pepper, like mushrooms]." (Tr.)

This reference seems to antedate by six to ten years the next mention of the tomato in the literature of western Europe.

Petrus Matthiolus was a physician by trade, but his chief claim to fame lies in the several editions of this literary work, which is nominally a commentary on the work of the botanist Dioscorides. Actually, these commentaries were greatly enriched. Some of the new plants, Arber notes, were Matthiolus' own observations, "but most of the species which he described for the first time were not his own discoveries." His correspondents, who made the major contributions of new species to the *Commentarii,* included a Turkish diplomat, Busbecq, and his personal physician, Quakelbeen; and also the famed physician, botanist and teacher, Luca Ghini, who founded the botanical garden at Pisa.

Just who was responsible for the observations on the tomato which appear in the *Commentarii* is not known. The briefness of the account makes it seem almost epistolary; on the other hand, it is apparently an observation made in Italy.

One of the most commonly quoted pieces of information on the early use of the tomato is the statement "that it is eaten in Italy with oil, salt, and pepper." Dozens of later authors, writing in every major western European language, repeat Matthiolus' observation.

1548—De Toni, G. B. "Spigolature Aldrovandiane. VI. Le piante dell'antico Orto Botanico di Pisa ai tempi di Luca Ghini." Annali di Botanica. Volume V. pp. 421–440. Roma, 1907.

The botanical garden at Pisa is the oldest such institution in the western world. This reprint of the manuscript catalogue of the 620 plants which were in the garden in 1548 does not include any plant identifiable as the tomato.

1554—Matthiolus, Petrus Andrea. Commentarii in libros sex Pedacii Dioscoridis Anazarbei, de medica materia. Venetiis, 1554.

p. 479. In chapter headed *Mandragoras* opp. marginal note, Matthiolus reports that "the eggplant is commonly eaten cooked in the manner of mushrooms, with oil, salt, and pepper."

This edition differs from the 1544 Italian version essentially only in that it mentions the Italian name for the tomato, "*Pomi d'oro,*" and its Latin equivalent, "*Mala aurea,*" and takes note of a red variety.

The following editions of the *Commentarii* [Venetiis] contain passages concerning the tomato identical to the one in the 1554 edition: 1558, p. 537; 1560, p. 537; 1570, p. 684; 1583, p. 425.

1550–1600—There are several herbarium specimens dating from this period:

1. Jerna, Gaetano. "Qualche Cenno di Storia sul Pomodoro in Italia." Humus. Volume III. No. 9. September, 1947.

p. 26. Jerna reports that there is a sheet labelled: *"Malus insana, Mandragorae species Poma amoris"*[2] in an herbarium in the Biblioteca Angelica di Roma attributed by Professor Emilio Chiovenda to Francesso Petrollini and dated between 1550 and 1560.

2. ————. In the same article, Jerna reports that in an index to an herbarium, preserved in the manuscripts of Ulisse Aldrovandi at Bologna, there is listed a specimen bearing the names: *"Malus insana altera, Poma amoris."* Professor Chiovenda attributes this herbarium to Petrollini also and assigns the same dates, 1550 to 1560, to its preparation.

3. Mattirolo, O. Illustrazione del Primo Volume dell'Erbario di Ulisse Aldrovandi. Genova, 1899.

p. 129. The sixteen-volume herbarium of Ulisse Aldrovandi, now preserved at the Botanical Garden of Bologna after many wanderings, is generally conceded to be the oldest extant herbarium in the world. Aldrovandi, a pupil of Luca Ghini, apparently began his collecting about 1551, and by 1570 had collected fourteen volumes. Specimen No. 368, in the first volume,[3] consists of a leaf and a small inflorescence and is labelled *"Pomum amoris. Mali insani species. Tembul quibusd."* Mattirolo describes the specimen as well preserved, but reports that it is on the sheet with two leaves of *"Cuccumis" Citrullus.*

Mattirolo states that most of the plants were collected in the vicinity of Bologna, although there are a few cultivated plants, a few plants from foreign countries and some alpines.

4. Michiel, Pietro Antonio. "I cinque libri di piante." Codice Marciano, 1551–1575.

Prof. Jerna (see 1 & 2 above) reports that in this "herbarium," which actually consists of colored illustrations of the plants, there is included (Libro Rosso I N. 46) a representation of a tomato. The illustration is labelled: *"Licopersico Galeni —pomodoro da volgari, poma amoris da alcuni et del Peru."* Its *virtu* is also described: "If I should eat of this fruit, cut in slices in a pan with butter and oil, it would be injurious and harmful to me." (Tr.)

5. Camus, J., and Penzig, O. Illustrazione del Ducale Erbario Estense del XVI secolo Conservato nel R. Archivio di Stato in Modena. Modena, 1885.

p. 35. Specimen 142 is labelled *"Pomi di Ettiopia ouer Pomi d'oro."*

This herbarium is dated by Camus and Penzig between 1570 and 1600.

1570—Pena, Petrus, and de l'Obel, Mathias. Stirpium adversaria nova . . . Londini, 1570.

pp. 108–109. (See Great Britain, 1570. Pena.)

1572—Gvilandinvs, Melchior. Papyrvs, hoc est commentarivs in tria, C. Plinj Maioris de papyro capita . . . Venetiis, 1572.

[2] The names attached to this specimen indicate that it may well be an eggplant rather than a tomato.

[3] The Aldrovandi specimen cited above is apparently the basis for the listing, "1551, Aldrovandi," appearing on p. 232 in P. A. Saccardo's *Cronologia della Flora Italiana.* (Padova, 1909.)

pp. 90–91. Guilandini discusses the plant which Galen has named *Lycopersion.* He suggests that the plant to which Galen refers may be one of three plants including the "*tumatle* of the Americans." He discusses each of these possibilities. Nothing is said directly concerning the use of the tomato, but it is noted that the juice of the *Lycopersion* of Galen, whatever that plant might be, was useful because of its cooling nature for rheumy joints and other such pains.

1581—de l'Obel, Matthias. Kruydtboeck oft beschrÿuinghe van allerleye ghewassen, kruyderen, hosteren, ende gheboomten. Antwerp, 1581.

p. 331. (See Central Europe, 1581. de l'Obel.)

1583—Caesalpinus, Andrea. De Plantis libri XVI. Florentiae, 1583.

p. 211. "*Mala insana* are rather round, like apples; we know two different kinds; one of golden color like *Malum Appium*; whence some call it "golden apple;" the other type squatty and broad, like *Malum roseum*, marked by furrows, reddish in color like flame . . . [they are] two or three cubits long . . . [their] flowers are white. Both of them are foreign; they are cultivated in gardens to look at more than to use. Some, however, eat their fruit prepared in dishes, as *Pyra insana*, [the egg plant], but they have a certain musky odor, particularly the red ones. I think they are related to certain types of *Solanum furiosum*." (Tr.)

About the preparation of *Pyra insana*, Caesalpinus says: "The fruits are eaten before ripe, thoroughly boiled or roasted in the manner of mushrooms. Its flavor imitates mushrooms, but not without strong condiments, such as pepper, in order to remove the wild flavor." (Tr.)

His reference to the white color of the tomato flower must be, generally speaking, incorrect.

1585—Durante, Castor. Herbario Nuovo. Roma, 1585.

p. 372. Pomi d'oro.

"They are cold, but not so cold as the Mandrake. They are eaten in the same way as the eggplant, with pepper, salt and oil, but afford little and poor nourishment." (Tr.)

While this volume is certainly not a translation of any one work, the section devoted to the *Pomi d'oro* is obviously of an eclectic nature. The passage quoted seems to be a slightly altered version of a similar statement in Dodonaeus (see Central Europe, 1574). Another section sounds like Matthiolus (1544, see above).

The 1602, 1607, and 1617 editions of *Herbario Nuovo* (published in Venice) also contain the passage quoted above, on p. 372.

1586—Camerarius, Ioachimus. De plantis epitome vtilissima, Petri Andreae durch . . . Ioachimum Camerarium. Franckfurt am Mayn, 1586.

pp. 378–379. (See Central Europe, 1586. Matthiolus.)

1586—Camerarius, Iiachimus. De plantis epitome vtilissima, Petri Andreae Matthioli . . . Francofvrti ad Moenvm, 1586.

p. 821. (See Central Europe, 1586. Camerarius.)

1588—Camerarius, Ioachimus. Hortvs medicvs et philosophicvs: in qvo plvrimarvm stirpivm breves descriptiones. Francofurti ad Moenum, 1588.

p. 130. (See Central Europe, 1588. Camerarius.)

1597—Gerarde, John. The herball or generall historie of plants. London, 1597.

p. 275. (See Great Britain, 1597. Gerarde.)

1613—Tabernaemontanus, Iacobus Theodorus. Neuw vollkommentlich Kreuterbuch . . . Franckfurt am Mayn, 1613.

Volume II. p. 494. (See Central Europe, 1613. Tabernaemontanus.)

1640—Parkinson, John. Theatrum Botanicvm. London, 1640.

p. 352. (See Great Britain, 1640. Parkinson.)

1651—Bavhinvs, Ioh., and Cherlervs, Ioh. Hen. Historia plantarvm vniversalis, nova, et absolvtissima cvm consensv et dissensv circa eas. Ebrodvni, Volume III, 1651.

Volume III. pp. 620–621. (See Central Europe, 1651. Bavhinvs.)

1666—Ambrosinus, Hyacinthus. Phytologiae hoc est de plantis partis primae tomus primus. Additis aliquot plantarum viuis iconibus . . . Bononiae [Bologna], 1666.

p. 86. "*Pomum amoris* is so named because amatory powers are attributed to it or because it has a fitting elegance or beauty worthy to command love." (Tr.)

1673—Ray, John. Observations made in a Journey through part of the Low Countries, Germany, Italy, and France. London, 1673.

pp. 406–407. Many fruits [the Italians] . . . eat which we either have not or eat not in England . . . including Love apples . . ."

Several other varieties of *Solanum* are mentioned in this work (pp. 235, 267, 277, 407). The quoted passage seems to be the only reference to the tomato.

1686—Raius, Joannes. Historia Plantarum. London, 1686.

Volume I, p. 675. (See Great Britain, 1686. Raius.)

1696—[Matthiolus, P. A.] Theatrvm botanicvm. Das ist: Neu vollkommenes Kräuter-Buch . . . erstens zwar an das Tagliecht gegeben von Herren Bernhard Verzascha, anjetzo aber in eine gantz neue Ordnung gebracht . . . durch Theodorvm Zvingervm. Basel, 1696.

pp. 896–897. (See Central Europe, 1696. Matthiolus.)

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. (See Great Britain, 1710. Salmon.)

1719—Tournefort, J. P. The Compleat Herbal of Mr. Tournefort. (Translated from the Latin with additions from Ray, Gerard, Parkinson, and others). London, 1719.

Volume I, p. 214. (See Great Britain, 1719. Tournefort.)

1721—Miller, Joseph. Botanicum Officinale; or a Compendious Herbal. London, 1721.

p. 32. (See Great Britain, 1721. Miller.)

1727—Boerhaave, Hermannus. Historia plantarum, quae in Horto Academico Lugduni-Batavorum crescunt . . . Romae, 1727.

Pars secunda, p. 509. (See Central Europe, 1727. Boerhaave.)

1731—Miller, Philip. The Gardeners Dictionary. First edition. London, 1731.

In alphabetical sequence under *Lycopersicon.* (See Great Britain, 1731. Miller.)

The 1737, 1741, 1748, 1752, 1759, and 1768 editions of this work contain references concerning the use of the tomato in Italy which are identical to that in the 1731 edition.

1737—Blackwell, Elizabeth. A Curious Herbal containing Five hundred Cuts of the most Useful Plants, which are now used in the Practice of Physick. London, Volume I, 1737; Volume II, 1739.

Volume I. Facing plate 133. (See Great Britain, 1737. Blackwell.)

1744—Zuingerus, Theodorus. Theatrum botanicum, das ist: Volkommenes Kräuterbuch . . . Itzo auf das Neue übersehen, und mit vielen Beschreibungen und Figuren der Kraüter vermehret durch Friedrich Zwinger, des seel. Authors Sohn, . . . Basel, 1744.

p. 1088. (See Central Europe, 1744. Zuingerus.)

1745–1775—Jerna, Gaetano. "Qualche Cenno di Storia sul Pomodoro in Italia." Humus. Volume III. No. 9. September, 1947.

p. 27. The author speculates as to the reasons why the tomato did not become immediately popular in Italy. He particularly wonders how the Neapolitans, in whose diet the tomato now forms such an important part, could have gotten along without the plant. Jerna apparently believes that some sort of aura of bad luck was cast around the plant much as it had been about the potato. He points out that the name "*Pomme d'Amour*" in itself suggests an aphrodisiacal quality in the fruits. Apparently the same quality was attributed to the potato. As to what broke down those barriers—Jerna suggests "probably the famous famines of 1745, 1771, and 1774 induced the people of southern Italy to take confidence in the tomato, much as it happened in Great Britain and France with the potato." (Tr.)

1755—Hill, John. The Useful Family Herball. Second edition. London, 1755.

p. 11. (See Great Britain, 1755. Hill.)

1769—Saccardo, P. A. I codici botanici figurati e gli erbari . . . Venezia, 1904.

A reprint of: Agosti, Giuseppe. Exercitationes botanicae per agrum Bellunensem, seu Plantarum in agro Bellunensi sponte nascentium vel arte excultarum . . . Two volumes. Belluni, 1769.

p. 14. letter c. *Lycoperisicon.* It is listed as a cultivated plant.

1776—Onomatologia Botanica Completa. Frankfurt and Leipzig, 1772–78. Volume VIII, 1776.

Volume VIII. p. 619. (See Central Europe, 1776. Onomatologia.)

1779—Linné, Carl von. Vollständiges Pflanzensystem nach der 13ten lateinschen Ausgabe und nach Anleitung des holländischen Houttuyschen Werks ubersetzt. [von G. F. Christmann und G. W. F. Panzer]. Nürnberg, 1779.

Volume V. pp. 681–683. (See Central Europe, 1779. Linné.)

1786—de la Lande, I. I. Voyage en Italie . . . Second edition. Paris, 1786.

Volume I. p. 510. "One also begins to find in Lombardy a fruit that is common in Rome, and which is slightly known in Paris: the *pommes d'oro, Pomidoro,* or *Tomate* of the Spaniards." (Tr.)

1787—Salat-Gewächse. Frankfurt am Main, 1787.

p. 197. (See Central Europe, 1787. Salat-Gewächse.)

1789—Rozier, François, Abbé, editor. Cours complet ou dictionnaire d'agriculture. Paris, 1789.

Volume VIII. p. 177. (See France, 1789. Rozier.)

1790—Sibly, E. Culpeper's English Physician and Complete Herbal. London, 1790.

p. 228. (See Great Britain, 1790. Sibly.)

1792—Walters, Johann Iacob. Gartenkunst. Stuttgart, 1792.

p. 118. Walters says that the tomato, like the eggplant, is eaten by the Spaniards, Portugese and part of the Italians and French.

1794—Dictionnaire des Plantes Usuelles. Paris, 1794.

Volume VI. p. 145. (See France, 1794. Dictionnaire.)

1796—Bechstein, Johann M. Kurzgefaste gemeinnutzige Naturgeschichte der Gewächse des In- und Auslandes. Leipzig, 1796.

Volume I. p. 333. (See Central Europe, 1796. Bechstein.)

1799—Jolyclerc, N. Phytologie Universelle. Paris, 1799.

Volume IV. p. 214. (See France, 1799. Jolyclerc.)

1802—Anonymous note. The Cultivator. New Series. Volume IX. Albany, N. Y., 1852.

p. 381. (See U. S., 1802. Anonymous.)

1804—Bianchi, ——. "Ueber den Anbau und Küchengebrauch der Tomatis, oder Liebesäpfel (*Solanum Lycopersicum* L.)." Allgemeines Teutsches Garten-Magazin. Volume I. Weimar, 1804.

p. 377. (See Central Europe, 1804. Bianchi.)

1811—Re, Filippo. L'Ortolano. Milan, 1811.

pp. 268–271. Three varieties of "*Pomidoro*" are listed and described: *P. Schiacciato; P. A. Peretto; P. Globoso.* Directions for their culture are given. Presumably these plants are being raised as food plants.

1811—Sickler, J. V. Garten-Handlexikon. Erfurt, 1811.

———. (See Central Europe, 1811. Sickler.)

1822—Loudon, J. C. An Encyclopaedia of Gardening. London, 1822.

p. 763. (See Great Britain, 1829. Loudon.)

1829—Loudon, J. C. · An Encyclopaedia of Plants. London, 1829.

p. 160. (See Great Britain, 1829. Loudon.)

1840—Dewey, Chester. Report of Herbaceous Flowering Plants of Massachusetts. Cambridge, 1840.

p. 166. (See U. S., 1840. Dewey.)

1841—Russell, J. W. "On the Culture of the Tomato and Egg Plant." Magazine of Horticulture. Volume VII. Boston, New York; 1841.

p. 97. (See U. S., 1841. Russell.)

1842—Anonymous. "The Tomato and its Uses." The Cultivator. Volume IX. Albany, N. Y., 1842.

p. 167. (See U. S., 1841. Anonymous.)

1853—Anonymous. "Notizen." Gartenflora. Volume II. Erlangen, 1853.

pp. 248–249. (See Central Europe, 1853. Anonymous.)

1857—Hassenstein, ———. "Ueber die Benutzung der Liebesäpfel." Gartenflora. Volume VI. Erlangen, 1857.

p. 54. (See Central Europe, 1857. Hassenstein.)

CENTRAL EUROPE

This designation includes the following major modern political units: Germany, Austria, Switzerland, The Netherlands, Belgium.

1553—Oelinger, Georg. Herbarium des Georg Oelinger. Anno 1553 zu Nürnberg. Edited by Eberhard Lutze and Hans Retzlaff. Salzburg, Akademischer Gemeinschaftsverlag, 1949.

Plate 44 pictures a tomato. The accompanying label lists the names: *Rote Tomate (Liebes-* oder *Goldapfel.), Solanum lycopersicum (Mala Aurea seu Poma Amoris.)* The authorship and dates of these names are not clear.

The plates in this modern edition are selections from the manuscript work, *Magnarum medicinae partium herbariae et zoographiae, imagines quamplurimae excellentes: a praeclaro in hoc studii genere viro, Domino Georgio Oelingero*

Norimbergensi, pharmacopola, mercatore et cive, mira perspiutate picturae et magnus sumptibus in hunc librum relatae, which is preserved (MS 2362) in the Manuscript Collection of the Library of the University of Erlangen. It consists of a series of hand-colored plant illustrations prepared for the Nürnberg apothecary, George Oelinger. The editors note that the work was in preparation for a number of years, and was finally finished for Oelinger about 1553 by a Samuel Quicchelberg.

There seems to be no doubt that tomatoes were known to Oelinger and his illustrators from plants grown in his own garden at Nürnberg. Gesner (see 1561 below) specifically lists Oelinger as one of the German gardeners cultivating this plant.

Whether the plant was grown primarily as a curiosity or for its medicinal properties is not clear. Oelinger was apparently a zealous plant collector, who, in the heyday of plant drugs, might have well mixed his pleasure in collecting rare plants with his business of selling simples. Perhaps his clients were willing to pay dearly for the latest "wonder drugs."

Plate 44, numbered S. 541 in the manuscript, is one of three tomato varieties illustrated. In the complete Oelinger work, in addition to the red variety, two yellow varieties are illustrated (S. 543 and S. 545).

1553—Dodonaeus, Rembertus. Trivm priorvm de stirpium historia commentariorum imagines ad viuum expressae. Antverpiae, 1553.

p. 428. This early work lists the Latin, German, and French names for the tomato along with an illustration of the plant. Nothing is said of the uses.

1554—Dodonaeus, Rembertus. Crüydeboeck. Antwerp, 1554.

pp. 471–472. See the Lyte translation of this work (Great Britain, 1578. Dodoens).

1558—Dodonaeus, Rembertus. Histoire des Plantes . . . Nouvellement traduite . . . en françois par Charles de l'Ecluse. Anvers, 1557.

See the Lyte translation of this work (Great Britain, 1578. Dodoens).

1561—Gesnerus, Conradus. Horti Germaniae. Argentorati [Strasbourg], 1561.

Reverse side of p. 273. *Pomum aureum vel amoris dictum* . . . ". . . the fruit is odorless, not unpleasant, not harmful in food; the size of a small . . . apple [and] round; often rather large, uneven and lumpy; [the fruit] is gold in one species, red in a second, and in a third white." (Tr.)

Gesner continues, noting that the fruit is easily grown [in Germany], and matures fruit early. The plant is described as flourishing in pots or borders with rich soil and plenty of water.

A list of the "German" gardeners who cultivate this plant is also furnished by Gesner. These include: 1. Öllingerus of Nürnberg; 2. Vuoysselus of Breslau; 3. Petrus Condenbergius of Antwerp; 4. Joachimus Kreichius of Torgau.

Ollingerus (Georg Oelinger), Gesner indicates, had died sometime before the publication of *Horti Germaniae*. In a discussion of prominent German gardeners (p. 243), including those listed above, Gesner reports that Oelinger ". . . cultivated a garden over a long period of time and with great interest, and he prepared for himself a volume with pictures of plants painted most elegantly . . ." (see 1553, Oelinger, above.)

1563—Dodonaeus, Rembertus. Crüydeboeck. Anvers, 1563.

p. 375. See the Lyte translation of this work (Great Britain, 1578. Dodoens).

1574—Dodonaeus, Rembertus. Pvrgantivm aliarvmqve eo facientivm, tvm et radicum, conuoluulorum ac deleteriarum herbarum historiae, libri IIII . . . Antverpiae, 1574.

p. 364. *De Aureis Malis.*

"They are frequently sown in gardens . . .

"Although they are cold, they are less cold than Mandrake. The apples are eaten by some prepared and cooked with pepper, salt, and oil. They offer the body very little nourishment and that unwholesome." (Tr.)

The reference to the consumption of tomatoes with pepper, salt and oil originated with Matthiolus (see Italy, 1533. Matthiolus). The evaluation of the fruit as cold and offering little nourishment is apparently Dodonaeus' own, and is frequently repeated by later authors.

Dodonaeus includes a mythological note in this section on golden apples: "There are other golden apples of which the poets tell, of the gardens of the daughters of the Hesperides, which were guarded by a dragon which Hercules killed." (Tr.)

1580—Kessler, H. F. "Landgraf Wilhelm IV von Hessen als Botaniker." Program der Realschule zu Cassel. Cassel, 1859.

p. 9. "Ludwig [Count Ludwig von Hessen (Marburg)] had bought on a trip to Heidelberg the seeds of the following plants and sent them on the 29th of February, 1580, to Cassel . . . *Poma amoris*." (Tr.)

There seems little doubt but that the tomatoes grown from those seeds were of interest to Wilhelm only as curiosities or perhaps as ornamentals.

1581—de l'Obel, Matthias. Kruydtboeck oft beschrÿuinghe van allerleye ghewassen, kruyderen, hesteren, ende gheboomten. Antwerpen, 1581.

pp. 331–333. *Gulden Appelen.*

"This foreign plant is also of double or doubtful nature: that is, of the nature of the Mandrake, the Nightshade, and yellow poppy: therefore it must be placed among these. Another reason it must be placed among these is because some people considered it, as well as the yellow poppy, to be a *Glaucium*, although it cannot be the latter (i.e. the yellow poppy); for no plant can be *Glaucium* if it has yellow juice; and as Dioscorides says no yellow poppy nor any *Chelidonie* [can be Glaucium], on account of their *(exulcererendé)* strength. Nor also can it be placed among the sorts of *Oenanthe*, which is the largest of the herbs which have yellow sap, for this is hot by nature. But rather should this *Glaucium* be the same as the plant which bears golden apples (i.e. the tomato)? This does not seem a sufficiently certain identification either. For it does not have one or two of the signs which

Dioscorides describes (in his discussion of *Glaucium*) i.e. of the sap and the leaves. The sap of the *Glaucium* is very useful for those who have running humours of the eye with heat; the white of the eye becomes grey when it is first put on, wherefore it is called in Latin, *Glaucium;* unless it was so called, as Pliny says, from the leaves which have the color of sea water. It [the tomato] not only drives away the power of superfluous dampness, but it tempers also the heat as has been put to the test by our modern doctors. Yes, it is also very good against wild fire (erysipelas), because it is very cold, diminishing the heat when it is applied. The sap that is drawn from the burning of branches (of *Glaucium*?) which grow in Syria and hot places is not too strong and is also thicker and brighter in color than that from the tomato. The juice of the apples (i.e. tomatoes) especially is watery, thin and yellowish, and like that of melons, and the leaves are also not dissimilar to those of the melon, for they are very long, winged, thick and similar to each other, quick growing and grey of color, cut, hollowed out, and hacked like cauliflower. The whole plant is very succulent and creeps along the earth like wild cucumbers and has the same yellow flowers and upstanding side branches: the fruit is very large and of the size and appearance of an orange, rounded and with furrows running from the stem-end, upwards, sometimes yellow and sometimes bright red like those of the balsam apple or foreign cherry, and containing yellowish, flat seeds. These apples were eaten by some Italians, like melons, but the strong stinking smell gives one sufficient notice how unhealthful and evil they are to eat. But it is emphatically not the *Glaucium* which the Venetians and other apothecaries of Italy use, as the modern herbalists think it is, because the outside of the fruit of that plant (i.e. *Glaucium*) is rosy and the inside yellow, bitter, and with an unlovely smell, thus having all the signs which Dioscorides lists. He lists these characteristics so that it should not be possible for the greedy Syrian Jews to counterfeit the *Glaucium*, as is done with very many other things: that is to counterfeit the smells, the colors and tastes as was done in the time of Dioscorides. Yes, what is more, the tomato can very well be used even if it is not the *Glaucium;* but it should not be considered the *Glaucium* for this reason. What is more, if I wanted to have a good convenient medicine at the beginning of the flux—one which would have a resolving power, I should rather draw-out a sap from a Dewthistle or Goosethistle or a Condrille which is uniquely stinking, milky, and yellowish, and use it unmixed for the things which Dioscorides cures with *Glaucium*, which should do the same good with more safety. For some of these are not very different in appearance and strength from Poppies and *Glaucium*.

"Another kind of *Poma amoris* which comes forth from Spanish seed sown in our gardens has erect stalke, one cubit in height and is similar in appearance to the aforementioned, but is smaller." (Tr.)

Then follows a discussion of the preparation and properties of *Glaucium* for medicinal use, as given by Dioscorides, and the medicinal properties of the plant as stated by Galen.

This Flemish reference is in need of a critical translation.

1583—Dodonaeus, Rembertus. Stirpium historiae pemptades sex. sive libri XXX. Antverpiae, 1583.

p. 455. This reference is identical to that contained in the 1574 *Purgantium* of the same author. (See 1574, Dodonaeus, above.)

The 1616 edition of this work (Antverpiae. pp. 457–458) contains essentially the same reference as the 1583 work.

1586—Matthiolus, Petrus Andreae. Kreuterbuch . . . gemehret vnd verfertiget durch . . . Ioachimum Camerarium. Franckfurt am Mayn, 1596.

pp. 378–379. *Gold öpffel, Poma aurea.* "They have become common in all gardens . . . In Italy the fruit is eaten cooked with pepper, oil and vinegar, but it is an unhealthy food, and gives little nourishment." (Tr.)

The fruit is also reported as efficacious for scabies when treated with oil or macerated in the sun. Uses of the juice of the plant in treating eye diseases, and for erysipelas and hot fluxes are discussed.

The following editions of this work contain a reference essentially identical to that quoted above: 1611—Frankfurt am Mayn. pp. 378–379; 1678—Basel. p. 678.

1586—Camerarius, Ioachimus. De plantis èpitome vtilissima, Petri Andreae Matthioli . . . Francofvrti ad Moenvm, 1586.

p. 821. *Poma amoris.* "It grows in gardens and likes moist places . . . It is cold and not without bad qualities. The apples are eaten without harm in Italy. They are also macerated with oil and dried in the sun there, or buried in horse manure, in order to anoint scabies, . . . this is highly praised by some." (Tr.)

The Francofurti ad Moenum, 1636, edition of this work also contains the reference quoted above.

1588—Camerarius, Ioachimus. Hortvs medicvs et philosophicvs: in qvo plvrimarvm stirpivm breves descriptiones. Francofurti ad Moenum, 1588.

p. 130. "*Pomum amoris* or *de oro,* called by the Milanese '*Pomum Indum,*' and by the foreign name '*Tumatle* from the island of Peru'." (Tr.)

Speaking generally of its uses, Camerarius says that the apples cooked in oil or dried in the sun are effective against scabies. From the context of the 1586 work by the same author (see above), it seems clear that this use is specific for Italy.

1591—Tabernaemontanus, Iacobus Theodorus. Neuw Kreuterbuch. Franckfurt am Mayn, Volume II . . . digerirt vnd vollbracht durch Nicholavm Braun, 1591.

Volume II. p. 464. "These apples have become common in gardens . . . The juice of this fruit is of a quite cold nature. It should not be used internally . . . Some say that the juice is good for St. Anthony's fire and other hot fluxes [when] spread on externally; however, one should take care with it, for it can soon do very great harm." (Tr.)

1601—Schvvenckfelt, Caspar. Stirpium & fossilium Silesiae catalogvs. Lipsiae [Leipzig], 1601.

p. 325. *Poma amoris.* "Its juice reacts strongly against erysipelas, St. Anthony's Fire and other warm fluxes." (Tr.)

The quoted material is probably taken from Pena and de l'Obel (see Great Britain, 1570. Pena). Whether or not this prescription was used in German is unknown.

1604—In a painting by Jan Brueghel the Elder titled "The Gifts of the Earth and Water," now part of the Vienna Art Collection, there appears what may well be a small pear or cherry-shaped variety of tomato. The painting is dated 1604.

1609—Durante, Castor. Hortulus Sanitatis. Das is ein heylasm [es] vnd nützliches Gährtlin der Gesundtheit . . . Nunmehr aber in vnsere hoch Teutsche Sprach versetzt durch Petrum Uffenbachium. Franckfurt am Mayn, 1609.

p. 557. *Goldtäpffel. Mala aurea. Poma aurea.* The reference to the use of

the tomato is a simple translation from the 1585 Italian *Herbario Nuovo* (see Italy, 1585. Durante).

1613—Tabernaemontanus, Iacobus Theodorus. Neuw vollkommentlich Kreuterbuch . . . Franckfurt am Mayn, 1613.

Volume II. p. 494. The reference is identical to that in the 1591 edition of the same work with the following pertinent additions:

a. ". . . others use the juice of the plant *(des Krauts)* for the eyes and look upon it as *Glaucium*." (Tr.) [For amplification of the relation between *Glaucium* and the tomato: See Central Europe, 1581. de l'Obel.]

"The apples boiled in oil or well macerated in the sun, are good against scabies *(hissige Räud)* smeared with it." (Tr.)

b. "In Italy, they eat the fruit cooked with pepper, oil and vinegar, but it is an unhealthy food and of little nourishment." (Tr.)

The Basel, 1664, edition of this work also contains the passages quoted above (*Das ander Theil.* p. 1174).

1635—Nierembergivs, Ioannes Evsebivs. Historia Natvrae. Antverpiae, 1635.

p. 319. The fruit is described as being used to make a pickle, and as bringing out the flavor of foods and stimulating the appetite. The leaves are recommended for a remedy for St. Anthony's Fire; vaporized or poulticed they are said to be good for diseases of the eyes and head. It is also a remedy for an upset stomach; and breaks up tumors of the ears when used with salt. The juice is recommended for inflammation of the throat and spreading ulcers. With certain compounds it is good for a children's disease called "*syrrhasin*." With egg white it fights acute fluxes and is good for ear aches. Etc. . . .

1644—Dodonaeus, Rembertus. Crvydt-Boeck. Antwerpen, 1644.

p. 750. An adequate translation of this Flemish work could not be obtained. The apples are reported as being cold, but not so cold as Mandrake. Some are reported to eat the apples cooked with oil, pepper and vinegar. It is said to be good for scabies.

1651—Bavhinvs, Ioh., and Cherlerus, Ioh. Hen. Historia plantarvm vniversalis, nova, et absolvtissima cvm consensv et dissensv circa eas. Ebrodvni, Volume III, 1651.

Volume III, pp. 620–621. "The juice of this plant is very useful for the cure of a rheum or defluxion of hot humours of the eyes which may occasion a glaucoma if not prevented. Not only does it restrain the afflux of the humor, but moderates fever . . . Furthermore, it is very effective against St. Anthony's Fire and erysipelas. The apples are eaten by some Italians just as cucumbers, but the whole plant exhales an evil odor; it is of little food value, and it is not very safely used as food. It yields moreover, very little food to the body, and that evil and corrupt. It is cold, but not so cold as Mandrake. Cooked in oil, it is efficacious against scabies. By a chemical preparation, it yields an oil very proper for the cure of [burnings] . . . This oil, rubbed on the temples and body induces sleep . . . " (Tr.)

1654—Laurembergivs, Petervs. Horticvltvra, libris II. comprehensa; . . . Francofurti ad Moenum, 1654.

Dürkop (see 1907, Dürkop, below) reports that the tomato is not listed in the seventh chapter of the second book of this work, which lists a large number of little-known vegetables.

1663—Becher, Joachim Matthaeus. Parnassus medicinalis illustratus. Ulm, 1663.

Dürkop reports the following verse from this work:

"Goldäpffel brauchet man, sie stillen bald den Grind,
Zum Essen innerlich man sie nicht gut befind."
(See 1907, Dürkop, below.)

1666—Chabraeus, Dominicus. Stirpivm icones et sciagraphia. Genevae, 1666.

p. 525. The tomato is listed under Class 34: Malignant and Poisonous Plants. In the appendix to the work, on p. 654, the plant is reported to be cold, but not so cold as mandrake, and the nourishment which it furnishes to the body is said to be small and corrupt.

The juice is said to be effective against certain humours, and as a remedy for erysipelas and St. Anthony's Fire. Cooked in oil the fruit is recommended for scabies, and certain chemically prepared oil extracts are said to be a cure for burnings. This same oil applied to the temples and body is reported to induce sleep.

1673—Nylandt, Petrus. De Nederlandtse herbarius, of Kruydt-Boeck . . . Amsterdam, 1673.

p. 507. *Gulden Appel. Appel der Liefde.*

The cooling quality of the plant is discussed, and it is noted that the fruit, cooked in oil, is effective against scabies.

1676—Cause, D. H. De Koninglycke Hovenier . . . Amsterdam, 1676.

p. 185. *Appel der Liefde, anders Gulde Appel.*

The plant is described in detail and careful directions for its culture are given, but nothing is said or implied concerning its uses.

1682—Munting, Abrahamus. Waare Oeffening der Planten. Amsterdam, 1682.

p. 522. *Gouden Appel.* The varieties of love apples are listed and their method of culture is described. Nothing is said of the use of this plant.

1684—Elsholtz, Johann Siegesmund. Vom Garten-Bau. 3 Druck. Cölln a. d. Spree, 1684.

The tomato is known to this author only as an ornamental. The plant is described in the second book (The Flower Garden) but it is not mentioned in the fourth chapter of the third book (An Enumeration of Kitchen Fruits)—Dürkop (see 1907, Dürkop, below).

1696—[Matthiolus, P. A.]. Theatrvm botanicvm. Das ist: Neu vollkommenes Kräuter-Buch . . . erstens zwar an das Tagliecht gegeben von Herren Bernhard Verzascha, anjetzo aber in eine gantz neue Ordnung gebracht . . . durch Theodorvm Zvingervm. Basel, 1696.

pp. 896–897. *Goldäpffel.* "The gold apples are cold and moist in nature; they have a saltpeter-like, volatile, somewhat oily taste, and through this the property to resolve, and to alleviate pains . . . In Italy the gold apple is eaten with pepper, oil and vinegar, but it is an unhealthy food . . .

"The juice of the plant, freshly pressed and warmed, when dropped in the eyes and covered with a little cloth, cures sharp, running fluxes; it also heals the scabies and the erysipelas when diligently applied . . ." (Tr.)

The plants are reported planted "in our gardens."

1706—Liger, Louis. Le Jardinier Fleuriste et Historiographe . . . Amsterdam, 1706.

Volume II. pp. 350–353. The method of cultivation and best mode of use of this plant as an ornamental are discussed in detail.

1715—Elsholz, Johann Siegesmund. Neuangelegter Garten-bau. Leipzig, 1715.

p. 94. The tomato is described among annual plants for the flower garden.

1727—Boerhaave, Hermannus. Historia plantarum, quae in Horto Academico Lugduni-Batavorum crescunt. Romae, pars I-II, 1727.

Pars secunda. p. 509. "The virtues of this plant are disputed and the controversy has not been resolved; but to me the plant would seem better referred to the poisonous plants than to the medicinal plants, for its seeds when taken upset the stomach and cause faintness and a sort of apoplexy." (Tr.)

1731—Boerhaave, Hermannus. Historia plantarum, quae in Horto Academico Lugduni-Batavorum crescunt. Londini, pars I, II, 1731.

Pars secunda. p. 509. The reference is identical to that in the Romae, 1727, edition above.

1744—Zuingerus, Theodorus. Theatrum botanicum . . . Itzo auf das Neue übersehen, und mit vielen Beschreibungen und Figuren der Kräuter vermehret durch Friedrich Zwinger, des seel. Authors Sohn, . . . Basel, 1744.

p. 1088. "The gold apples [possess] the property of cooling, of dispersing and of soothing, pains . . .

"The juice, freshly pressed from the plant *(aus dem Kraut)* when dropped into the eyes and bound with a cloth, heals sharp, running fluxes; it also heals *Ueberrothe* and the *wilde Feuer.*" (Tr.)

This work also reports that the tomato is eaten in Italy cooked with salt, pepper and vinegar, but adds that it is an unhealthy food.

1748—Möller, Georg F. "Versuch, den Ursprung der Augen in den Gewächsen zu erklären." Hamburgisches Magazin. 3rd Band, erstes Stück. Hamburg, 1748.

pp. 119–120, paragraph 24. This article contains a discussion of the so-called "augen" in *poma amoris* or *Lycopersicon.* This may be the first non-taxonomic scientific work involving the tomato.

1751—Dale, Samuel. Pharmacologia, seu manuductio ad materiam medicam: . . . Quinta editio, ex scriptis Hermanni Boerhaave . . . Lugduni Batavorum, 1751.

p. 188. It is noted that the fruit is used medicinally, its strength being similar to *Solanum* and *Mandragora* (probably the nightshade and the mandrake). Uses and qualities reported by other authors are listed.

1754—Erhart, Balthasar. Oeconomische Pflanzenhistorie nebst dem Kern der Landwirtschafft Garten- und Arzneykunst. Ulm and Memmingen, Volume III, 1754.

Volume III. p. 171. The tomato is listed as a poisonous plant in the same category as the nightshade and belladona.

1774—Reuss, Christianus Friedericus. Compendium Botanices. Ulm, Stettin, 1774.

p. 211. *Solanum Lycopersicon . . . "ad acetaria."*

Apparently *ad acetaria* refers to the use of the fruits with vinegar and oil or as salad (see Harper's *Latin Dictionary*).

1776—Onomatologia Botanica Completa. Frankfort and Leipzig, 1772–78. Volume VIII, 1776.

Volume VIII. p. 619. "Their [the tomato's] berries are round, generally furrowed and red, sometimes without furrows or yellow or white. People ascribe to them, especially to the berries, a stupefying power which borders on the fancied strength of the love potion; however, this belief has not been confirmed by actual experience, and since in addition to this, in Italy and India the fruit is preserved with vinegar or in saltwater, and frequently eaten without harm as a salad *(Salat)* or "spice" *(Gewürz)*, all of these beliefs appear to be invalidated. One can easily propagate them in the garden through seeds, where they must be kept in pots." (Tr.)

1779—Linné, Carl von. Vollständiges Pflanzensystem nach der 13 lateinschen Ausgabe und nach Anleitung des holländischen Houttuynschen Werkes übersetzt [von G. F. Christmann und G. W. F. Panzer]. Nürnberg, 1779.

Volume V. pp. 681–683. *Liebes-Aepfel.* "The fruits are thought poisonous by some persons, but are freely eaten in the East Indies; also eaten in Italy with pepper, salt and oil like melons." (Tr.)

1784—Plenck, J. J. Bromatologia seu doctrina de esculentis et potulentis. Viennae, 1784.

p. 126. The author says that the plant is thought poisonous, but it is his opinion that the fruit can be safely eaten when cooked in sauces.

1787—Salat Gewächse. Frankfort am Main, 1787.

p. 197. *Solanum lycopersicum, Liebesäpfel.* This is one of the plants listed under the heading, *"Salatarten zum Kochen."*

"In Italy and India the fruit is preserved with vinegar and saltwater and frequently eaten without harm as a salad *(Salat)* or 'spice' *(Gewürz)*." (Tr.)

1788—Anonymous. "Von den Sommergewächsen." Journal für die Gärtnerey. Volume XIII. Stutgart, 1788.

p. 498. "Several of these summer plants are desirable because of their flowers, others on account of their pretty fruits and seed capsules; a few only because of their distinctly colored foliage are planted in the flower garden, or because of their tenderness in pots. To the second group belong[s] . . . *Solanum lycopersicum* . . ." (Tr.)

p. 513. "*Solanum Lycopersicum* [is also in a special group] which on account of its pretty fruit is planted in pots" (Tr.)

1791—Schkuhr, Christian. Botanisches Handbuch. Wittenberg, 1791.

Volume I. p. 145. "These [tomato] fruits are held by some as poisonous. [They are eaten in several ways in various parts of the world, but are grown] as ornamentals in German gardens." (Tr.)

1796—Bechstein, Johann M. Kurzgefaste Gemeinnutzige Naturgeschichte der Gewächse des In- und Auslandes. Leipzig, 1796.

Volume I. p. 333. "The fruits are generally considered as poisonous." (Tr.) The author also reports that the fruit is used in Italy, Portugal, Spain and Bohemia with salt, oil and pepper, also in gravies and sauces to which it gives a pleasant taste.

1804—Willdenow, Carl L. Anleitung zum Selbstudium der Botanik. Berlin, 1804.

p. 167. "In our gardens it [the tomato] is planted for the sake of variety. In southern Europe and in America people use the large red fruit prepared in various ways." (Tr.)

1804—Bianchi, ——. "Ueber den Anbau und Küchengebrauch der Tomatis, oder Liebesäpfel (*Solanum Lycopersicum* L.)." Allgemeines Teutsches Garten Magazin. Volume I. Weimar, 1804.

p. 377. (Extract from a letter from Mr. Bianchi at Rudolfstadt.) "As promised, you are receiving in the accompanying box, several tomato fruits, the seeds of which I brought back from Italy. I have sown them in April, as you have seen for yourself, in the open garden, in good soil and in sunny place, and transplanted them in May . . .

"In Italy and France they are used in the kitchen in the following way: namely, when they are ripe, which one can tell by their red color and softness, they are cooked for about a half hour in a little bouillon or, that lacking, in a little water; crushed and run through a sieve, to free broth from seeds and skin. This broth is used in soups, ragouts, *potagen*, *pasteten*, and other sauces in order to give them an acid flavor.

"The fruits I am sending you are not quite ripe. The ripe fruits can't be sent very well, for through the long journey the inner flesh [of the fruit] turns into juice, and the skin becomes so thin that one can hardly handle it without it bursting, and they are certainly savory!

Bianchi" (Tr.)

A footnote to this letter indicates that the large red-fruited variety has earned a place among the ornamental plants in Germany. It is said to have come to Germany from the south.

1805—Encyclopedia von Krünitz. Berlin, 1805.

100th part. This work reports that the tomato is mostly grown for decoration in the garden or in pots. It adds that many people consider it poisonous, but points out that it is eaten elsewhere in the world. Only in recent times, says the Encyclo-

pedia, have the Germans been giving greater consideration to the culture of the tomato as well as to its use in the kitchen.—Dürkop. (See 1907. Dürkop, below.)

1805—B., F. J. "Garten Miscellen." Allgemeines Teutsches Garten-Magazin. Volume II. Weimar, 1805.

p. 294. ". . . Die Alten schreiben den Aepfelchen einen verliebten Wahnwitz zu."

1809—Dietrich, F. G. Vollständiges Lexicon der Gärtnerei und Botanik. Weimar, 1809.

Volume IX. pp. 318–319. The tomato is described as fairly common in German gardens. The fruits are considered poisonous by some, but in warmer countries, where they attain a great degree of ripeness, they are eaten with oil, salt and pepper and are also used in soups and other dishes.

1821—Land- und Garten Schatz. Stuttgart, 1821.

Dritter Theil. p. 161. *Von einjährigen Gewächsen.* The tomato is listed in this section of the work. Its fruits are described as being used, in part, in the kitchen.

1834—Anonymous. Review of *L'Horticulteur Belge.* Volume I. Brussels, 1833. The Gardener's Magazine, Volume X. London, 1834.

p. 445. "Tomatoes, when ripe, may be preserved a year in a strong solution of salt in water, without boiling, or any culinary preparation whatever. When taken out of the brine for use, they must be steeped some hours in fresh water."

1847—Schnizlein, Adalbert. Die Flora von Bayern. Erlangen, 1847.

p. 201. *Lycopersicum esculentum.* A footnote describes this as an "ornamental" and as "occasionally cultivated plants."

1853—Anonymous. "Notizen." III. Der Liebesäpfel als Pflanze des Kuchengartens." Gartenflora. Volume II. Erlangen, 1853.

pp. 248–249. "The love apple . . . belongs to the best-liked plants of the garden in France, Spain, Italy and the greatest part of America. The fruits of this plant are used not only as ingredients in many different kinds of dishes, but they are also brought to the table in the form of compotes and sauces, or mixed with bread as a vegetable. In America they are attributed with strengthening the stomach . . . The taste of this fruit has something peculiar about it, so that one must get used to it, then it belongs to one of the most pleasant dishes. You may now ask why this plant is almost not cultivated in Germany and Switzerland or only as an ornamental. We can give the assurance that the love apple prospers with us and that only ignorance of its useful properties, or the fearful retention of old handed-down prejudices [which hold] that the fruits of the love apple are inedible or even harmful: these are the reasons why it still isn't planted.

"We admit, however, that if the love apple is not properly cultivated its fruits remain small and have a bad taste." (Tr.)

1857—Hassenstein, ______. "Ueber die Benutzung der Liebesäpfel." Gartenflora. Volume VI. Erlangen, 1857.

p. 54. "In many places, particularly in southern lands, the fruits of the *Solanum Lycopersicon* (Love-apple) are used to a considerable extent, partly by

themselves with pepper, oil and salt, partly for sauces. The first use will probably find little [favor] with us; on the other hand, the use for sauces and ragouts is much to be recommended." [A method of preparation designed to cultivate a taste for tomatoes follows.]

1877—Schmidlin, E. Gartenbuch. Fourth edition. Edited by Th. Nietner and Th. Rümpler. Berlin, 1877.

p. 449. "This annual ornamental [the tomato] is of great economic importance in southern countries, and has been recently cultivated by us on account of its beautiful fruit which not only displays a bright color, but also can be used as a stewed fruit, in which form it is used as an ingredient in foods and as a sauce, etc." (Tr.)

1879—Rümpler, Th. Illustrierte Gemuse- und Obstgärtnerei. Berlin, 1879.

p. 286. "The love apple with its showy fruit is still much too little cultivated in the kitchen gardens of Germany. For the most part, one finds it cultivated as an ornamental, [planted] on slopes or between large boulders where it thrives extraordinarily well and yields many fruit, quite early, especially when planted in southern aspects.

"Most people don't know the right way to . . . [get acquainted] with the splendid fruit of the tomato; usually they let themselves be frightened on the first trial, because of the initial unpleasant smell, reminiscent of the nightshade. But it is a fact that after the first conquest of this fear, it soon finds great favour in food. One should emphasize that dishes prepared out of tomatoes do not speak well in its behalf, because people, as with the eggplant, don't know the right way of preparing them." (Tr.)

1882—Anonymous. "Neue und empfehlenswerthe Pflanzen." Gartenflora. Volume XXXI. Erlangen, 1882.

pp. 115–116. *Abgebildet im Kataloge von Chr. Lorenz in Erfurt.* (2) *Lycopersicum esculentum* . . . "It is a generally known plant, used as a kitchen garden plant and also as an annual ornamental. On the basis of the fruit shape I have distinguished three forms . . .:

"a. typicum . . . It is the sort which is found everywhere in cultivation; its fruit is preferred for use in sauces and as a 'spice' for foods, be it in the fresh condition or preserved. Earlier the fruit was used chiefly only in France, but now they are generally used, especially in restaurants.

"b. *cerasiforme (Kirschenartiger Liebesapfel)* . . . It is used more as an ornamental than as a plant for the kitchen garden.

"c. *pyriforme (Birnförmiger Liebesapfel)* . . . It is still infrequent in culture." (Tr.)

1900—Hegi, Gustav. Illustrierte Flora von Mittel-Europa. V Band, 4 teil. München, 1927.

p. 2608. "This South American plant, especially during the last decade, has been frequently cultivated with us in the numerous cultivated forms, for its edible fruits." (Tr.)

1907—Dürkop, Wilhelm. "Ein Beitrag zur Geschichte der Tomate." Naturwissenschaftliches Wochenschrift. Volume XXII. No. 35. Jena, September 1, 1907.

pp. 548–550. This author presents a brief survey of the literature pertinent to the history of the origin, development, cultivation, and use of the tomato.

FRANCE

1558—Dodonaeus, Rembertus. Histoire des Plantes . . . Nouvellement traduite . . . en François per Charles de l'Ecluse. Anvers, 1558.

See the Lyte translation of this work (Great Britain, 1578. Dodoens).

Just how much this French translation of the original Flemish edition of Dodoens' Cruydeboeck (Antwerp, 1554) reflects conditions in France is doubtful. Both author and translator, though Flemish by birth, were extremely cosmopolitan; yet there is no evidence that their work applies beyond the borders of Flanders.

1582—Estienne, Charles, and Liebault, Jean. L'Agriculture et Maison Rustique. ——, 1582.

p. 241. See the English translation of this work (1600. Stevens, below).

The tomato is not mentioned in the 1567, Paris, or 1572, Montluel, editions of the work.

1587—Dalechamps, Iacqves. Historia generalis plantarum, in libros XVIII . . . Lvgduni [Lyon], 1587.

p. 628. Pomum Amoris, sive Aureum. (See 1615, Dalechamps, below.)

1600—Stevens, Charles, and Liebault, John. Maison Rustique, or The Countrie Farme. Tr. into English by Richard Surflet. London, 1600.

p. 253. Opposite marginal note "Golden Apples."

"Within this small time there hath been seen a plant somewhat like unto apples of love egg plant, bearing a round fruit like an apple, divided upon the outside as a melon is with furrows; in the beginning it is green, but afterwards when it cometh to ripeness, it becometh somewhat golden and sometimes reddish. This plant is more pleasant to the sight than either to the taste or smell, because the fruit being eaten provoketh loathing and vomiting."

Note the resemblance of the first part of this reference to Matthiolus, 1554. (See Italy, 1544. Matthiolus.)

The London, 1616, and Rouen, 1658, editions of this work carry the same reference.

1615—Dalechamps, Iacqves. Histoire generale des plantes, contenant XVIII livres . . . faite Française par Me Iean des Movlins. Lyon, 1615.

p. 533. Des Pommes d'Amour ou Pommes d'Or. "They grow readily in the garden from seed . . . The apples, like the entire plant, are cold; however, a little less than the Mandrake; wherefore it is dangerous to use. However, some eat the apples cooked with oil, salt, and pepper. They give very little nourishment to the body, and that bad and corrupt . . ." (Tr.)

The following editions of this work contain the reference quoted above: 1587, Lugduni [Lyon]. p. 628 (see 1587, Dalechamps, above); 1653, Lyon. p. 533.

1619—de Serres, Olivier. Le théâtre d'agriculture. 1619.

"Their fruits [the tomato] are not good to eat." The author says that the plants are commonly used in France for covering garden houses and arbours.—Dürkop. (See Central Europe, 1907. Dürkop.)

1739—Chomel, J. B. Catalogus plantarum officinalium secundum earum facultates dispositus. Parisiis, 1739.

p. 110. *Pomme Dorée, ou Pomme d'amour* is listed in a section of the catalog title, "*Plantae Narcoticae.*"

1739—Chomel, J. B. Abregé de l'Histoire des Plantes Usuelles. Cinquieme edition. Paris, 1739. Three volumes.

Tome second. p. 789. "This plant is about of the same quality as the mandrake, but for internal use, less dangerous; for in some parts of Europe, among others in Italy, its fruit is eaten preserved with vinegar, or salt or pepper; it is a bad enough food. I know of persons who steep the fruit in olive oil which they then use for contusions, tumors, rheumatism, and sciatica. It is a good enough *resolutif* and anodyne. The juice of the entire plant is used externally in inflammation of the eyes and other parts; one applies it in fomentations; one can use it in cataplasms like the leaves of the ordinary morelle." (Tr.)

1750—D., M. C. Chef de Cuisine de M. le Prince de *** Dictionnaire des Alimens, Vins et Liqueurs. Paris, 1750.

pp. 101–105. On these pages are several recipes involving the use of tomatoes.

1760—Bois, Désiré. Les Plantes Alimentaires chez tous les Peuples et à travers les Ages. Paris, 1927.

Volume I. pp. 323–331. It is reported that in the catalogue of seeds of the House of Andrieux Vilmorin, the tomato was still classed under the heading "ornamental plants." Not until the 1778 catalogue was it admitted to the ranks of vegetable seeds.

1763—Liger, Louis. Le Jardinier Fleuriste. Paris, 1763.

p. 178. (See Central Europe, 1706. Liger.)

1770—Buc'hoz, P. J. Traité Historique de Plantes que croissent dans la Lorraine et les Trois Evêchés. Paris, 1770.

Volume X. p. 397. *Pomme d'amour* . . . The medicinal qualities of the plant are described, and the author adds that "some eat the fruits in salads with salt, oil, pepper and vinegar, but," he notes, "they are of little nourishment and bad juice." (Tr.)

1770—Buc'hoz, P. J. Dictionnaire Raissoné Universel des Plantes, Arbres et Arbustes de la France. Paris, 1770.

Volume III. p. 42. *Pomme d'amour* . . . "People regard its fruit as poisonous and narcotic; they make little use of them, cultivating them only for the beauty of their berries." (Tr.)

1778—(See 1760, Bois, above.)

1783—Le Bon Jardinier, Almanach pour l'Annee M.DCC. LXXXIII. Paris, 1783.

p. 64. *Tomate. Pomme d'amour. Solanum Lycopersicon.*
Brief cultural directions are given. Sauces are said to be made from the fruit.

The plant is listed among the kitchen garden vegetables.

1785—Miller, Philip. Dictionnaire des Jardiniers. Translated from the eighth edition of Philip Miller's 'Gardeners Dictionary.' Paris, 1785.

Volume IV. In alphabetical sequence under *Lycopersicon.* The reference is essentially the same as that in the English seventh edition of 1759. (See Great Britain, 1759. Miller.)

1785—Le Berryais, L. R. Traité des Jardins. Nouvelle ed. Paris, 1785.

Volume II. p. 397. "The fruit when fully ripe develops an agreeable acid. It would be dangerous to make use of it before it has acquired this acidity."

1789—Rozier, François, Abbé, editor. Cours Complet ou Dictionnaire d'Agriculture. Paris, 1789.

Volume VIII. p. 177. *Pomme d'amour ou Tomates.* "The fruits when quite ripe are used in sauces for all kinds of foods, and the expressed juices are preserved for winter use by the addition of salt and a little vinegar. Seasoned with oil, vinegar and salt, the fruits form a delicate and refreshing food . . . In Italy, in Spain, in Provence, and in Languedoc, the fruit of the tomato is very much sought after." (Tr.)

1792—Walters, Johann Jacob. Gartenkunst. Stuttgart, 1792.

p. 118. (See Italy, 1792. Walters.)

1794—Dictionnaire des Plantes Usuelles. Paris, 1794.

Volume VI. p. 145. The reference is essentially identical to that contained in M. Chomel's *Abregé de l'Histoire des Plantes Usuelles.* Paris, 1739. (See 1739, Chomel, above.)

1797–1798—Lamarck, J. B. A. P. M., chevalier de. Encyclopédie Methodique. Botanique. Paris, 1797/1798.

Volume IV. p. 287. *Morelle pomme d'amour . . . tomato.* "Cultivated in Portugal, Spain, and southern France. Fruits used in sauces and when young, conserved in vinegar. When one eats too many of them, he experiences a slight sharp and stinging taste." (Tr.)

1799—Jolyclerc, N. Phytologie Universelle. Paris, 1799.

Volume IV. p. 214. *Pomme d'amour.* "The fruits of the *Lycopersicon* are suspected to be poisonous. People believe these plants to be narcotic, as the *Solanums* and the Mandrake; they are very little used in medicine. The fruits give off, it is true, a disagreeable odor; however, the Italians eat, with impunity, quantities of them cooked in butter. This is a proof that the cooking removes from them the narcotic and poisonous agent." (Tr.)

1801—Boutelou, Claudio, and Boutelou, Estéban. Tratado de la Huerta. Madrid, 1801.

pp. 375–383. (See Spain, 1801. Boutelou.)

1802—Dumont de Courset, G. L. M., Baron. Le Botaniste Cultivateur. Paris, 1802.

Volume II. p. 130. "S. *Lycopersicum* is cultivated in southern France for its fruits from which are made soups that have the color of the juice of the 'écrevisse'." (Tr.)

1802—Anonymous note. The Cultivator. New Series. Volume IX. Albany, N. Y., 1852.

p. 381. (See U. S., 1802. Anonymous.)

1804—Bianchi, ——. "Ueber den Anbau und Küchengebrauch der Tomatis, oder Liebesäpfel (*Solanum Lycopersicum* L.)." Allgemeines Teutsches Garten-Magazin. Volume I. Weimar, 1804.

p. 377. (See Central Europe, 1804. Bianchi.)

1822—Loudon, J. C. An Encyclopaedia of Gardening. London, 1882.

p. 763. (See Great Britain, 1822. Loudon, below.)

1822—Albert, B. Manuel Complet d'Économie Domestique. Second edition. Paris, 1822.

p. 7. A recipe for *Marmelade des Tomates.*
p. 11. A recipe for *Sauce Tomate.*
p. 284. A recipe for preserving tomatos.

1825—Noisette, Louis. Manuel Complet du Jardinier. Paris, 1825.

Volume II. p. 446. *Tomate.* "Everybody today knows the use of its [tomato's] red fruit, which is round or oval, smooth or furrowed, according to variety."

1825—Archambault. Le Cuisinier Economie. Third edition. Paris, 1825.

p. 265. *De la Pomme-d'amour ou Tomate.* "The chief use one makes of it is in sauces; and I will indicate the way I have seen them prepared in Provènce." (Tr.)
A recipe for *Pommes d'amour Farcies* follows.

p. 357. A recipe for preserving tomatoes.

1828—Descourtilz, M. E. Flore Pittoresque et Medicale des Antilles, ou Traite des Plantes Usuelles. Paris, 1828.

Volume VI. p. 95. *Morelle Pomme-d'Amour. (Anti acoustique émolliente.)* "The tomato is cultivated in America and in Europe, particularly in Portugal, in Spain and in the central part of France. The resources which it offers to the culinary art in the preparation of ragouts and '*coulis*,' have given it admittance to all the vegetable gardens in the vicinity of Paris. Its paste is conserved for the winter, by means of drying; then, when the vegetable resources are limited, in the middle of the winter, the tomato sauce appears on our tables in a thousand ways—to serve in beef

or mutton soups, to be associated with codfish and many other varieties of fish. One eats it in the colonies with piment and other aromatics to prevent inertia in the stomach. One preserves tomatoes in vinegar while they are young. Its culture demands a rich soil and humidity . . ." (Tr.)

Its juice is described as being used macerated in oil and applied to contusions, rubbed in oil on rheumatic parts or applied to inflammations of the eyes and ears. Its leaves are said to be used in a cataplasm. The pulp is recommended for other eye inflammations.

1828—Anonymous. "Notes and Reflections made during a Tour through Part of France and Germany in the Autumn of the Year 1828." The Gardener's Magazine. Volume VII. London, 1831.

pp. 9–10. "December 24, 1828. The forcing department of the Versailles kitchen garden is not without interest . . . Kidney beans were in a growing state, and a stock of young tomato plants were ready to transplant into their pots to fruit during the winter, the fresh fruit being wanted throughout the year for soups, stews and sauces . . . some pits contained excellent lettuces; and we were told that, between the pits and open gardens, kidney beans, lettuces and tomatoes were supplied every day in the year."

1829—Loudon, J. C. An Encyclopaedia of Plants. London, 1829.

p. 160. (See Great Britain, 1829. Loudon.)

1841—Russell, J. W. "On the Culture of the Tomato and Eggplant." Magazine of Horticulture. Volume VII. Boston, New York; 1841.

p. 97. (See U. S., 1841. Russell.)

1842—Anonymous. "The Tomato and its Uses." The Cultivator. Volume IX. Albany, N. Y., 1842.

p. 167. (See U. S., 1842. Anonymous.)

1845—Cosson, E., and Germain, E. E. Flora Descriptive et Analytique des Environs de Paris. Paris, 1845.

Volume I. p. 274. The tomato is listed and described as being "frequently cultivated in kitchen gardens."

1848—Dictionnaire Universel d'Histoire Naturelle. Dirigé par Charles d'Orbigny. Paris, 1848.

Volume XII. p. 600. *La Tomate Comestible* . . . "This plant today is one of the most common plants in our kitchen gardens . . . Everybody knows the daily use which one makes of these fruits, on account of their juice with its agreeable acidity, which is put into nearly all dishes as a seasoning. One uses the juice principally in its fresh state when the plant bears and ripens fruit, that is to say, during a large part of the summer and until frost.

"But one also uses extracts more or less concentrated, which one reduces to the state of a dry paste for the needs during the rest of the year." (Tr.)

1882—Anonymous. "Neue und empfehlenswerthe Pflanzen." Gartenflora. Volume XXXI. Erlangen, 1882.

pp. 115–116. (See Central Europe, 1882. Anonymous.)

1856—Moitessier, Albert. Essai sur les propriétés des Solanées et sur leurs principes actifs. Montpellier, 1856.

p. 64. "The Tomate is largely used in France both as food and seasoning and no ill effects are observed from it; nevertheless it is found that the use of these fruits, especially when overripe, is sometimes followed by colic or diarrhoea. The active principle appears to be located in the seeds, or the pulp which surrounds them." (Tr.)

1900—Curé, J. B. J. Les Jardiniers de Paris et leur Culture à travers les Siecles. Paris, 1900.

p. 209. "The Tomate is a relatively new plant in France, although undoubtedly grown in the gardens of the great and rich people long before it was raised commercially." (Tr.)

GREAT BRITAIN

This designation includes the following major political units: England, Ireland, and Scotland.

1570—Pena, Petrus, and de l'Obel, Matthia. Stirpivm adverstria nova . . . Londini, 1570.

pp. 108–109. (See Central Europe, 1581. de l'Obel.)

(The reference to the above edition of this work is essentially similar to that in the *first* paragraph of the quoted material in the 1581, *Kruydtboeck.* The 1576 Antwerp edition of the *Stirpivm Adversaria nova* is identical to the London 1570 edition, as is the 1605 London edition.)

1578—Dodoens, Rembert. A nievve herball, or historie of plantes: . . . First set fourth in the Doutche or Almaigne tongue, by that learned D. Rembert Dodoens . . . and nowe translated out of the French into English, by Henry Lyte Esquyer. London, 1578.

pp. 439–440. Of Amourous Apples or Golden Apples. "This is a strange plant and not found in this country except in the gardens of some herborists, where as it is sown . . . The complexion, nature and working of this plant is not yet known, but by that I can gather of the taste, it should be cold of nature, especially the leaves, somewhat like unto the Mandrake, and therefore also it is dangerous to be used."

This reference seems to have been translated and published without essential alteration from the de'Ecluse French version (Antwerp, 1557) of Dodoens' *Cruydeboeck* (Antwerp, 1554.)

1586—Dodoens, Rembert. A new herball or historie of plantes: . . . First set fourth in the Douch or Almaigne tongue, by that learned D. Rembert Dodoens . . . and now first translated out of the French into English, by Henry Lyte Esquier. London, 1586.

p. 508. With respect to the sections quoted, this reference is identical to that contained in the 1578 edition of this work. (See 1578, above. Dodoens.)

1597—Gerarde, John. The Herball or Generall Historie of Plantes . . . London, 1597.

p. 275. "Apples of Love do grow in Spain, Italy and such hot countries from whence myself have received seeds for my garden where they do increase and prosper.

"It is sown in the beginning of April in a bed of hot horse dung after the manner of musk melons and such like cold fruits . . .

"The golden apple with the whole herb itself is cold, yet not fully so cold as Mandrake, after the opinion of Dodonaeus; but in my judgement it is very cold, yea perhaps in the highest degree of coldness; my reason is because I have in the hottest time of the summer cut away the superfluous branches from the mother root, and cast them away carelessly in the allies of my garden, the which (not withstanding the extreme heat of the sun, the hardness of the trodden allies, and at that time when no rains at all did fall) have grown as fresh where I cast them as before I did cut them off; which argueth the great coldness contained therein. True, it is that it doth argue also a great moisture wherewith the plant is possessed, but as I have said, not without great cold, which I leave to every man's censure.

"In Spain and those hot regions, they used to eat the apples, prepared and boiled with pepper, salt and oil; but they yield very little nourishment to the body and the same naught and corrupt.

"Likewise they do eat the apples with oil, vinegar and pepper mixed together for sauce to their meat, even as we in these cold countries do mustard."

Gerarde is said to have relied heavily upon the *Pemptades* of Dodoens (see Central Europe, 1583. Dodonaeus). Certainly there are echoes from that work in this reference; nevertheless, it is substantially original. It is definitely known that Gerarde grew the tomato in his famous garden at Holborn (see 1599, below).

The 1633 and 1636 editions of this work (pp. 345–346) contain essentially the reference quoted above.

1599—Catalogus Arborum, Fruticum ac Plantarum tam Indigenarum quam Exoticarum, in Horto Johannis Gerardi cuius & Chirugi Londinensis Nascentium. Londini, 1599.

p. 16. This catalogue lists two varieties of the Apple of Love, the red and yellow. There is in the British Museum a unique copy of a 1596 edition of the catalogue of the plants in Gerarde's garden which the bibliographer has not seen.

1600—Stevens, Charles, and Liebault, John. Maison Rustique, or the Countrie Farme. Tr. into English by Richard Surflet. London, 1600.

p. 323. (See France, 1600. Stevens.)

The London, 1616, edition of this work contains the same reference (p. 253).

1622—Gunther, Robert T. Early British Botanists and their Gardens. University Press, Oxford, 1922.

p. 50. "John Goodyer in 1622 (March) received seeds of 22 garden plants from Coys, including two kinds of 'apples of love' or tomatoes."

The "Coys" referred to is a William Coys whose garden at Essex was said to rival that of Gerarde.

p. 379. According to a notation next to *Pomum amoris parvum* in Goodyer's list of plant names, Coys grew this variety of tomato in his garden.

What use either of these gentlemen made of the plants or fruit is not known.

1629—Parkinson, John. Paradisi in Sole. London, 1629.

pp. 379–380. *Pomum Amoris.* Love Apples. "Although the beauty of this plant consisteth not in the flower, but fruit, yet give leave to insert it here, lest otherwise it have no place; whereof

there are two especial sorts, which we comprehend in one chapter, and distinguish them by *maius* and *minus*, greater and smaller: yet of the greater kind we have nourished up in our gardens two sorts, that differ only in the color of the fruits and nothing else . . .

"They [Great Apples of Love (of) the ordinary red sort and the Yellow Amorous Apples] grow naturally in the hot countries of Barbary and Ethiopia; yet some report them to be first brought from Peru, a Province of the West Indies. We only have them for curiosity in our gardens and for the amorous aspect or beauty of their fruit . . .

"In the hot countries where they do naturally grow, they are much eaten of the people, to cool and quench the heat and thirst of their hot stomachs. The apples, also boiled, or infused in oil in the sun, are thought to be good to cure the itch, assuredly it will allay the heat thereof."

The *minus* variety may be our common cherry tomato (*L. esculentum*, s. sp. *Galeni*).

Parkinson's reference to the tomato as a cure for the itch is not original with him. It appears as early as Pena and de l'Obel, 1570 (see above).

1640—Parkinson, John. Theatrum Botanicum. London, 1640.

pp. 352 and 354. *Poma amoris* . . . Apples of Love . . . "(It) groweth in those easterly countries of Egypt, Syria, Arabia . . . The golden apples or apples of love are cold and moist, more than any of the former, and therefore are less offensive; these are eaten with great délight and pleasure in hotter countries, but not in ours, because their moisture is flashy and insipid for want of sufficient heat of the sun in their ripening."

1653—Culpeper, Nicholas. The English Physitian enlarged. London, 1653.

Redcliffe N. Salaman, in *The History and Social Influence of the Potato* (University Press, Cambridge, 1949) points out (p. 108) the omission of the potato, the jerusalem artichoke and the tomato from the Culpeper herbal. Says Salaman: "We may, I think, safely assume that not one of the three plants was sufficiently accessible as to be worth discussing in a book primarily devoted for the use of the ordinary intelligent household."

When the tomato does appear in one of the later editions of this work (see 1790, Sibly, below) profound medicinal properties are attributed to it.

1660—Sharrock, Robert. The History of the Propagation and Improvement of Vegetables. Oxford, 1660.

p. 4. Apples of Love are listed in a catalogue of plants that can be increased by seeds.

1665—Rea, John. Flora seu de Florum Cultura. London, 1665.

p. 196. *Pomum amoris* . . . "These plants are received only for the beauty of the Apples or Berries as they are commonly called, the flowers being not considerable. Sow in beginning of April and water, or else winter will take them."

1673—Ray, John. Observations made in a Journey through part of the Low Countries, Germany, Italy, and France. London, 1673.

pp. 406–407. (See Italy, 1673. Ray.)

1683—Sutherland, James. Hortus Medicus Edinburgensis, or a Catalogue of the Plants in the Physical Garden at Edinburgh. Edinburgh, 1683.

p. 322. Lists the red and gold apples of the love. The red variety is described

as having medicinal uses, although they are not specifically stated. The gold form is described as having no medicinal value.

1686—Raius, Joannes. Historia Plantarum. London, 1686.

Volume I. p. 675. "Sown in our gardens . . . The juice of this plant is very useful for the cure of a rheum or defluxion of hot humour of the eyes which may occasion a glaucoma if not prevented. However, it not only stops the afflux of the humour, but moderates and allays the inflammation . . .

"The apples are eaten by some in Italy prepared with pepper, salt and oil, as we eat cucumbers."

Ray also points out that the whole plant smells bad and is not very safely used as a food. The juice, according to him, is unpleasant and the nourishment the fruit offers the body is corrupt.

He adds that the fruit cooked in oil is effective against scabies and that by chemical preparation it yields an oil effective for burnings.

1710—Dale, Samuel. Pharmacologia, seu Manuductio ad Materiam Medicam. Iterata editio. Londini, 1710.

p. 270. *Poma amoris.* It is described as sown in gardens, flowering in summer. The fruit is the part of the plant which is used medicinally, its virtues being similar to *Solanum* and *Mandragora* (probably nightshade and mandrake).

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. Of Love Apples. "They grow naturally in hot countries, as in Ethiopia, Barbary, Egypt, Syria, Spain, Italy, and other hot countries: some report they were first brought to us from Peru; and I have seen them grow in Carolina which is the south-east part of Florida; but with us in England they grow only in gardens, where being nourished up, they bring forth their fruit to perfection . . .

"The whole plant and apples are cold and moist, almost in the fourth degree; but not so cold as mandrakes. They are cephalick, stomatick, nephritick, and uterine; of an attenuating, cleansing, repercussive, and anodine quality; and operate only as alteratives . . . They are peculiar to allay the heat of inflammations, but more especially of an erysipelas . . .

"The shops keep nothing of this plant; but you may have from it, 1. the apples themselves. 2. the juice. 3. an essence. 4. a cataplasm. 5. an oil. 6. a balsam for wounds . . .

"The apples. In Spain, and those hot countries, they use to eat the apples prepared and boiled in vinegar, with pepper and salt, and served up with oil, and juice of lemons: likewise they eat them raw, with oil, vinegar, and pepper, for sauce to their meat, as we here do cucumbers; but they yield not much nourishment, but only please and cool or quench the heat and thirst of hot stomachs.

"The juice. Applied upon inflammations, but especially bathed upon an erysipelas, and linen cloths wet in the same, laid thereon, abate the inflammation, and take away the preternatural heat.

"The essence. It represses vapors in women, is good against fits of the mother, opens the obstructions of the urine, taking away the heat and scalding thereof; is good against sand, gravel, and the stone, and gives ease in all pains proceeding from a hot cause. Dose from j to ij ounces.

"The cataplasm. It is good against the headache, megrim, gout, sciatica, and all pains whatsoever proceeding from a hot and dry cause: in outward applications it ought to be renewed twice a day.

"The oil. It cures all manner of burnings, and scaldings, whether of fire, water, oil, lead, etc. and has the virtues of the cataplasm, and may be annointed upon those places where a cataplasm cannot be applied.

"The balsam. It is a singular good thing to cool inflammations in wounds and ulcers, heal all sorts of burnings and scaldings, cleanse old running sores, and to give ease in the gout, pain in the

back, or any other part proceeding from vehement hot and fiery hot humors: it admirably heals wounds, and when cleansed, ulcers also, after the manner of preparations from *all-heals*.

"A special note. It appears that this plant abounds with a vast humidity; for in the hottest time in summer, the superfluous branches being cut off from the mother root, and carelessly cast away in the allies of the garden, though at a time when no rain shall fall, yet will they grow as fresh, as if they had not been cut off; which shows indeed the exceeding moisture of the herb.

1719—Tournefort, J. P. The Compleat Herbal of Mr. Tournefort. (Translated from the Latin with additions from Ray, Gerard, Parkinson, and others.) London, 1719.

Volume I. pp. 214–215. "The juice of this plant is very useful for the cure of rheum or defluxion of hot humors of the eyes, which may occasion a Glaucoma if not prevented: for it not only stops the afflux of the humour, but moderates and allays the inflammation: it is no less beneficial in a St. Anthony's Fire, and such like inflammatory distempers . . .

"The fruit boiled in oil is efficient for the cure of the itch and by a chemical preparation yields an oil very proper for the cure of burnings.

"The Italians eat the apples as we do cucumbers with pepper, oil and salt. Some eat them boiled; but considering their great moisture and coldness, the nourishment they afford must be bad."

1721—Miller, Joseph. Botanicum Officinale, or a Compendious Herbal. London, 1721.

p. 32. *Amoris Pomum* . . . "In Italy they eat these Love Apples with oil and vinegar, as cucumbers are eaten here, but they are seldom eaten with us, being of the nature of the othér *Solanums;* and therefore only used outwardly in cooling and moistening applications, in inflammations and erysipelas; and its juice especially is commended in hot defluxions of rheum upon the eyes. It is but seldom used."

1724—Bradley, Richard. A General Treatise of Husbandry and Gardening. (For the Months of August and September, and the remaining part of the second year.) London, 1724.

p. 181. "To Mr. Bradley. Sir. According to your desire, I send you a Catalogue of such curious Flowers as blow in my Garden from July to compleat the Year. I am,

Your humble Servant,
Thomas Fairchild."

p. 183. In the list which Mr. Fairchild sends along we find "Tree Love Apples, two sorts."

————. A General Treatise of Husbandry and Gardening. (For the months of June and July, the second year.) London, 1724.

p. 80. Under the heading "Flowers for the month of July," Love-Apples are listed.

1728—Bradley, Richard. Dictionarum Botanicum. London, 1728.

Volume II. In the appendix of this work: *Pomum amoris:* "The *Love Apple* is of various kinds, of the nightshade tribe: the fruits of all of them are hot and invigorating; the Capsicum and the Borongella are of this race; and are used in hot countries, in sauces to their meats. Every sort that I have seen makes an agreeable plant to look at, but the fruit of most of them is dangerous. They may, however, be raised from seed, for the sake of their pretty appearance, by sowing their seeds in March or April."

1730—Index Plantarum Officinalium, quas, ad Materia Medicae Scientiam Promovendam in Horto Chelseiano. Societas Pharmaceutica Londinensis. Londini, 1730.

p. 70. *Pom Amoris*. Fruits. This is another case where the tomato was grown for its fruits which were used medicinally.

1731—Miller, Philip. The Gardener's Dictionary. First edition. London, 1731. Folio.

In alphabetical sequence under *Lycopersicon*, Miller describes a technique for growing the plants for the flower border, and for potting. Concerning the latter, he says:

> "These plants which are placed in pots should be often watered, otherwise they will come to little (for they are very droughty plants); but when they are planted in a rich moist soil, they will grow to a prodigious size and produce large quantities of fruit, which in autumn when they are ripe, make an odd figure; but the plants emit so strong an effluvium as renders them unfit to stand near an habitation, or any other place that is much frequented; for upon their being brushed by the clothes they send forth a very strong disagreeable scent.
>
> "The Italians and Spaniards eat these apples as we do cucumbers with pepper, oil and salt; and some eat them stewed in sauces, etc., but considering their great moisture and coldness, the nourishment they afford must be bad. The first of these plants [a yellow variety] is the sort directed for medicinal use by the College in their Dispensatory."

The following editions of this work also contain the reference quoted above: 1737—Third edition. Folio; 1741—Second edition. Octavo (three volumes abridged); 1748—Third edition. Octavo (three volumes abridged).

1731—Boerhaave, Hermannus. Historia plantarum, quae in Horto Academico Lugduni-Batavorum crescunt . . . Londini, pars I, II, 1731.

Pars Secunda, p. 509. The reference is identical to that in the Romae 1727 edition (see Italy, 1727. Boerhaave).

1732—Meager, Leonard. The New Art of Gardening with the Gardener's Almanack. Second edition. London, 1732.

p. 123. In the Garden Almanack (for the Flower Garden) for March, the author directs that *Pomum amoris* be sown in the hotbed. They are also listed under flowers blowing in September (p. 133) and in October (p. 135).

1734—Miller, Philip. The Gardeners Kalendar. London, 1734.

p. 59. Love Apples are listed among the plants to be sown in the hot-bed during March.

p. 130. Love Apples are listed among the plants to be transplanted during June from the hot-bed into the borders of the flower garden.

1737—Blackwell, Elizabeth. A Curious Herbal containing Five Hundred Cuts of the most Useful Plants which are now used in the Practice of Physick. London, 1737.

Volume I. Facing Plate 133. "It is sown in gardens and flowers in July, the fruit being ripe in September. Love Apple, outwardly applied, is esteemed cooling and moistening, good for inflammations and erysipelas; the juice is commended in hot defluctions of rheum upon the eyes. In Italy they eat them with oil and vinegar as we do cucumbers."

1739—Rand, Isaacus. Horti Medici Chelseiani Index Compendarius. Londini, 1739.

p. 122. Five varieties of tomatoes are listed. Presumably they were being cultivated as medicinal plants.

1752—Miller, Philip. The Gardener's Dictionary. Sixth edition. London, 1752.

In alphabetical sequence under *Lycopersicon.* Several important additions appear in this edition:

"The Italians and Spaniards eat these apples as we do cucumbers, with pepper, oil and salt; and some eat them stewed in sauces, &c., and in soups they are now much used in England, especially the second sort, which is preferred to all the other. This fruit gives an agreeable acid to the soup; though there are some persons who think them not wholesome; from their great moisture and coldness, and that the nourishment they afford must be bad. They are called by the Portugese and Spaniards, *Tomatoes.* The first of these plants [a yellow variety] is the sort directed for medicinal use by the College in their Dispensatory."

This is the first documentation of any extensive culinary use of the tomato in Great Britain. The 1759 (seventh) edition of this work is identical in respect to the passages quoted. Extensive notes on the cultivation of the plants have, however, been added.

Miller describes how the seeds should be sown and the young plants cared for:

"In May, these plants should be transplanted either into pots filled with rich light earth or into borders near walls, pales, or hedges, to which their branches may be fastened to support them from trailing on the ground, which they otherwise will do, and then the fruit will not ripen, so that where these plants are cultivated for the sake of their fruit, they should be planted to a warm aspect, and the branches regularly fastened as they extend that the fruit may have the advantage of the sun's warmth to forward them, otherwise, it will be late in the season before they are ripe, and they are unfit for use before; but when the plants are brought forward in the spring, and thus regularly trained to the south sun, the fruit will ripen by the latter end of July, and there will be a succession of it till the frost kills the plants.

"Some persons cultivate these plants for ornament, but their leaves emit so strong offensive an odour on being touched, which renders them very improper for the pleasure garden, and their branches extend so wide and irregular as to render them very unsightly, for they cannot be kept within bounds, especially when they are planted in good ground, therefore the borders in which these plants are placed for their fruits must not be too rich, for in moderate soil they will be not so luxuriant and more fruitful."

1755—Hill, John. The Usefull Family Herbal. Second edition. London, 1755.

p. 11. Apples of Love. "The plant is a kind of nightshade, we cultivate it in gardens . . . The Italians eat the fruit as we do cucumbers. The juice is cooling; it is good externally used in eruptions on the skin and in diseases of the eyes, where a sharp humour is troublesome."

1765—Mr. Stevenson. The New and Complete Gardener's Kalendar. Dublin, 1765.

p. 128. March. Work to be done in the Kitchen Garden. "Sow . . . the seed of capsicum for pickling, and tomatoes for soups on a hot-bed."

p. 135. May. Work to be done in the Kitchen Garden. "Transplant for the end of the month, and in favourable weather, the tomatos for soups, and the capsicums for pickling, which have been raised upon hot-beds. Plant the tomatos near a wall, pale, hedge, or espalier to which the plants when grown must be fastened . . ."

This is the sole reference to the tomato in Ireland in the bibliography. The work seems to have certain similarities to the 1759 edition of Miller's *Gardeners Dictionary* (q. v.) as far as this plant is concerned.

1790—Sibly, E. Culpeper's English Physician and Complete Herbal. London, 1790.

pp. 227–228. Love-Apple. "It groweth into a tree of a reasonable height, with large dented leaves, cut in upon the edges, and of a pale green colour. The blossoms are large and white, which falling, the fruit follows . . . The tree is a native of Ethiopia; but it is planted in the gardens of many of the curious in this kingdom . . . The apples of love are under Venus; yet are they cold and moist in an extreme degree. They are olygotrophic and cachochymic; yet in hot countries, they are eaten as a sauce, boiled with pepper, salt and oil. The juice boiled with uxungia to a salve, heals all inflammations and burnings; and the leaves boiled with oil-olive, till crisped, then strained and afterwards boiled with wax, rosin, and a little turpentine, to a salve, are an infallible remedy for old sores and ulcers of the privities, or for wounds and ulcers in other parts of the body, coming of heat, or the vicious humours of the blood."

An illustration of the plant and fruit appears in plate No. 8, facing page 223.

The description of the plant, while it apparently intends to describe a tomato, is grossly incorrect. One can only surmise the effectiveness of the ointments which Mr. Sibly prescribes. (See 1653. Culpepper, above.)

1797—Mawe, Thomas. Every Man his Own Gardener. London, 1797.

p. 157. March. Work to be done in the Kitchen Garden. "About the middle of this month is the time to sow some tomatoes or love-apple seed; the fruit or apples of these plants are in some families much used in soups, and are also often used to pickle, both when they are green and when ripe."

Love-apples are also listed several times as plants suitable for the flower garden.

1801—Boutelou, Claudio, and Boutelou, Estéban. Tratado de la Huerta. Madrid, 1801.

pp. 375–383. (See Spain, 1801. Boutelou.)

1807—Martyn, Thomas. The Gardeners' and Botanists' Dictionary of the late Philip Miller, corrected and newly arranged with additions. London, 1803–07. Four volumes.

Volume II, Part II (1807). In alphabetical sequence under *Solanum*. Except for the change in the genus name, this edition adds nothing new to the older editions of Miller (see 1741, 1748, 1752, 1759, above).

1819—Sabine, Joseph. "On the Love Apple or Tomato . . . Transactions of the Royal Horticultural Society. Volume III. London, 1819.

pp. 342–354. "The great use which has been made of the Tomato of late years for culinary purposes, has occasioned it not only to be grown in private gardens, but has also rendered it an object of cultivation for the market of the metropolis. Possessing in itself an agreeable acid, a quality very unusual in ripe vegetables, it is quite distinct from any other product of the kitchen garden. It appears to be used, when fresh, in a variety of ways in soups and sauces; and its juice is preserved for winter use, in the manner of ketchup."

1820—Phillips, Henry. Pomarium Britannicum. London, 1820.

pp. 235–40. Reports (p. 236) that "The fruit has long been used by the wealthy Jew families in this country and within these last few years it has come into great use with all our best cooks, as it possesses in itself an agreeable acid, a very unusual quality in ripe vegetables, and which makes it quite distinct from all garden vegetables that are used for culinary purposes in this country. It makes a good pickle, and is preserved in various ways for winter use, and is made into a kind of ketchup also. When boiled in soups and sauces, it imparts an acid of a most agreeable flavour; it is also served at the table boiled or roasted and is sometimes fried with eggs. Love apples are to be seen in great abundance at all our vegetable markets; but I do not find that they are used by the middle or lower classes of English families who have yet to learn the art of improving their dishes with vegetables.

"Mr. John Wilmot, of Isleworth, states that in 1819, he gathered from six hundred plants, four hundred and thirty-three bushels, and that he then had many to spare. He adds that the plants produced from twenty to forty pounds weight each, and that some of the apples measured twelve inches in circumference."

1822—Loudon, J. C. An Encyclopaedia of Gardening. London, 1822.

p. 763. Section XI. Plants used as Preserves and Pickles. Paragraph 1404: "When ripe the fruit which has an acid flavor is put into soups and sauces, and the juice is preserved for winter use like ketchup; it is also used in confectionary, as a preserve; and when green as a pickle. Though a great deal used in England in soups and as a principal ingredient in a well known sauce for mutton; yet, our estimation and uses of the fruit is nothing to those of the French and Italians, and especially the latter. Near Rome and Naples, whole fields are covered with it, and scarcely a dinner is served up in which it does not in some way or other form a part . . ."

The above reference also appears in the 1827 edition of this work.

1826—Anderson, John. ". . . Receipts . . . procured for us by Mr. John Anderson F. H. S., Gardener to the Earl of Essex at Cassiobury, from an eminent French cook lately in the Earl's service." The Gardener's Magazine. Volume I. London, 1826.

p. 353. Seven recipes are listed including:

1. Tomata sauce for cold meat.
2. Potted tomata.
3. Tomatas quite plain [these are actually cooked].
4. Tomatas with gravy.
5. Tomatas pickled.
6. Towit of tomatas [a jam-like substance].
7. Tomatas as a dried fruit.

1827—M'Murtrie, Wm. "On the Utility of gathering unripe Tomatoes, and maturing them on Shelves in Hot-houses." The Gardener's Magazine. Volume VII. London, 1831.

p. 195. The author, who was gardener to Lord Anson, Shugborough Gardens, describes a technique for ripening green tomatoes by picking them and storing them on shelves in hot-houses. He adds, "The consumption at Shugborough is about two bushels a year, which are produced by about 80 plants." (Read April 5, 1827.)

1829—Loudon, J. C. An Encyclopaedia of Plants. London, 1829.

p. 160. S. *Lycopersicum.* "It is cultivated extensively around Naples and Rome for the use of the berry in sauces, stewing and soups. It is one of the most common articles used in Italian cookery and makes an excellent sauce for fish, meat and general purposes. Its use for sauce is greatly on the increase, and it is cultivated to a considerable extent near London, against walls and artificial banks, being raised on a hot-bed, and transplanted like other tender annuals."

The following editions of this work also contain the reference quoted above: 1841—London; 1855 and 1866—Edited by Mrs. Loudon. London.

1831—Phillips, Henry. The Companion for the Orchard. London, 1831.

pp. 225–227. The reference in this work is essentially identical to that in the *Pomarium Britannicum* of the same author. (See 1820 above. Phillips.)

1831—S., E. "On a mode of cultivating the Tomato, so as to make sure of ripening the Fruit without artificial Heat." The Gardener's Magazine. Volume VIII. London, 1832.

p. 174. "Sir, It having fallen to my lot to be placed in situations requiring a good supply of love apples, I have been induced to try a variety of methods to bring them to the greatest degree of perfection . . . [and if people follow this technique] we shall not (at least in this part of the country) hear of people being obliged to cut the fruit and hang it up in a warm room to ripen. [Sow the seeds indoors and grow the plants as large as possible before planting them out.] By growing the tomato plant as large as possible before planting out, they have the advantage of the summer for ripening, and by planting only one in each place, the small place usually left between the fruit trees may be used for them. Whereas by growing three in a pot (as is usually practised) they make a great deal of room and require continual cutting which causes them to push afresh, etc. I am, Sir, yours, & c. E. S. Tottenham, Dec. 24, 1831."

At least on the big estates, love apples seem to be a dietary item of some importance. Gardener E. S. seems a little annoyed at Mr. M'Murtrie's suggestion that one should ripen green tomatoes indoors (see 1827, above).

1832—Anonymous. "Covent Garden Market." The Gardener's Magazine. Volume VIII. London, 1832.

p. 624. On September 17, 1832, tomatoes were selling for 2*s* 6*d* per ½ sieve at the Covent Garden Market. They are listed under the heading: "Stalks and Fruits for Tarts, Pickling, etc."

1834—Anonymous. "On the Different Modes of Budding; and of Herbaceous, or Summer Grafting." (From *L'Horticulteur Belge.*) The Gardener's Magazine. Volume X. London, 1834.

p. 312. ". . . Tomatoes may be grafted in this manner on potatoes, and it is said that potato plants thus treated produce good crops both of potatoes and tomatoes."

This grafting experiment still remains an item of popular interest.

1836—Dickens, Charles. The Posthumous Papers of the Pickwick Club. Charles Scribner's Sons. New York, 1924.

Part II. p. 88. "And now, gentlemen, but one word more. Two letters have passed between

these parties, letters which are admitted to be in the handwriting of the defendant, and which speak volumes indeed. These letters, too, bespeak the character of the man. They are not open, fervent, eloquent epistles, breathing nothing but the language of affectionate attachment. They are covert, sly, underhanded communications, but, fortunately, far more conclusive than if couched in the most glowing language and the most poetic imagery—letters that must be viewed with a cautious and suspicious eye—letters that were evidently intended at the time, by Pickwick, to mislead and delude any third parties into whose hands they might fall. Let me read the first:—'Garraway's, twelve o'clock. Dear Mrs. B.—Chops and Tomato sauce. Yours, PICKWICK.' Gentlemen, what does this mean? Chops and Tomato sauce! Gentlemen, is the happiness of a sensitive and confiding female to be trifled away, by such shallow artifices as these?"

1840—Dewey, Chester. Report on the Herbaceous Flowering Plants of Massachusetts. Cambridge, 1840.

p. 166. (See U. S., 1840. Dewey.)

1842—B., C. "On the Culture of the Tomato or Love Apple *(Lycopersicum esculentum)* so as to insure a Crop in cold Situations and dull wet Seasons." The Gardener's Magazine. Volume XVIII. London, 1842.

pp. 277–279. "Of this plant which is a native of South America, and was introduced into this country in the year 1596, there are three or four varieties . . . Of these, the red-fruited is held in the highest estimation, on account of its superior size and beauty. It is cultivated [in several places in Europe] as well as in our own country, making an excellent sauce for fish, meat, &c. It is cultivated to a considerable extent near London, there being scarcely a gentleman's garden, either large or small, in which the love-apple may not be found growing and bearing fruit in abundance; although very often the fruit will not come to maturity . . . owing in a great measure . . . to the seeds not being sown early enough . . ."

The author then describes a method of giving the plants an early start by sowing them indoors in December and transplanting them. But evidently he had had trouble convincing others of the value of this technique. He comments:

"You will be surprised to hear that there are gardeners, even in these days of cheap knowledge, who will not profit by the labour of others either by reading or observing, but must go on in their own often obsolete way, yet such is the fact; for if anything new and rather out of the common way be shown them in the shape of drawings, articles, on culture, etc., they will flatly tell you they are deceptions, and that they want no 'new-fangled systems.' Many gardeners that have seen my love-apple plants this year will say: 'Bless me! you are precious soon with the tomatoes. Why, they will be a great deal too soon,' etc. I say: 'How so? What time do you sow your seed?' 'Oh! not before March or April.' 'What sort of a crop had you last year?' I ask. 'Oh! I got none, they did not ripen; they were too late.' So you see, they will show their own blindness. 'Well! will you have a few plants?' 'Oh! yes, I will take a few; I begin to see you are right.' Now it is evident by my neighbors' own account that the method is worth a trial; because last year they had no fruit themselves, and I had a good crop, and a few to spare to give away. I am sorry that some are so very sceptical, and think too much of their own ways; to such I would say, 'Give things a fair trial, and prove before you condemn'."

1858—Hogg, Robert. The Vegetable Kingdom and its Products. London, 1858.

p. 547. The Love Apple or Tomato. "The plant has a disagreeable and nauseous odor, and its juice evaporated over the fire produces a vapor so powerful as to cause vertigo and vomiting. A fruit is extensively used in Spain, Italy and France, and its cultivation is increasing in England and will become wider when people discover the agreeable ways in which the fruit can be prepared."

1870—Brotherston, R. P. "About Tomatoes." Garden. Volume 83. Feb. 22, 1919. London.

p. 86. ". . . The old fashioned ribbed tomatoes, one of the greatest of which was named Trophy, were atrocious in flavour and in smell. Not only has the tomato been improved as a cropper and in the beautiful smoothness and rotundity of its fruit, but along with these, the

sweetness of its flesh as opposed to its former peculiarly nasty taste is very remarkable. Nearly fifty years ago I had charge of a collection of tomatoes in pots . . . It may be interesting to note that plants from seeds sown in January were gathered in May. But the crops were small. How little the tomato was appreciated may be gathered from the fact that the crop was almost entirely consumed—raw—by myself. Nobody ate raw tomatoes in those days!"

The consumption of the tomato raw must be much more recent in England than its use as a cooked vegetable. It may well be possible that few if any people ate the tomato raw in England at this late date.

1880—Hall, Charles A. "Lore of the Tomato." The Gardeners' Chronicle. Volume 126. Third Series. London, 1949.

p. 54. "When I was a small boy, say seventy years ago, it was commonly said that a taste for tomatoes had to be acquired—no one liked them at the first eating. Actually, they never appeared on the table in my home and there was only one garden in our village where they were grown as a novelty. I saw them in all their glory of red and yellow fruitage and felt that fruits so attractive in appearance must be good to eat. I was tempted to help myself to one and alas! I fell. Great was my disgust when I came to taste it, for it was utterly nauseous to me and I quickly spat my mouthful out.

"My next taste of tomatoes was in Canada, where one bought them by the measure, not weight. I found I liked them and, on very hot days, bought them by the quart for a few cents, feeling their juice to be a good thirst quencher.

"Talking with folk of my own generation, I find that most of them in their youth looked upon taste for the fruit as one to be acquired. A lady acquaintance used to tell me how she, with a few friends, was shown over the gardens of a nobleman's estate in the north on which there was a house with ripe tomatoes. The head gardener told the party they might eat as many of the fruits as they liked, but not one of them got beyond the first mouthful. The good man evidently banked on the 'acquired taste' idea and he had gathered that none of his visitors had tasted tomatoes before. That would be about seventy-five years ago."

1886—De Candolle, A. Origin of Cultivated Plants. Second edition. London, 1886.

pp. 290–292. Pertinent references from this work are included in this bibliography.

1925—Dicks, S. B. "The Tomato." The Gardeners' Chronicle. Third Series. Volume 77. London, 1925.

p. 98. "The atmosphere of mistrust which surrounded this fruit in the time of Lyte (1578) still persisted at the end . . . of two centuries, and some traces still remain."

1943—Luckwill, L. C. "The evolution of the cultivated tomato." Journal of the Royal Horticultural Society. Volume 68. London, 1943.

pp. 19–25. Pertinent references from this work are included in this bibliography.

1943—Luckwill, L. C. The genus *Lycopersicon.* An historical, biological and taxonomic survey of the wild and cultivated tomatoes. Aberdeen University Studies, No. 120. Aberdeen, 1943.

Pertinent references from this work are included in this bibliography.

1948—Jenkins, J. A. "The origin of the cultivated tomato." Economic Botany. Volume II, Number 4. October–December, 1948.

pp. 379–392. The author presents a brief survey of the early history of the tomato, primarily to establish the origin of the plant. In the course of the article, several references to the use of the tomato are made; these all appear in this bibliography.

SPAIN AND PORTUGAL

1581—de l'Obel, Matthias. Kruydtboeck. Antwerpen, 1581.

pp. 331–333. (See Central Europe, 1581. de l'Obel.)

1597—Gerarde, John. The Herball or Generall Historie of Plants. London, 1597.

p. 275. (See Great Britain, 1597. Gerarde.)

1707—Sloane, Hans. A Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica. London, 1707.

Volume I. pp. 237–238. (See West Indies, 1707. Sloane.)

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. (See Great Britain, 1710. Salmon.)

1731—Miller, Philip. The Gardener's Dictionary. First edition. London, 1731.

The 1731, 1737, 1748, 1752, and 1759 editions of this work contain the same reference concerning the use of the tomato in Spain and Portugal. (See Great Britain, 1731 and 1752. Miller.)

1783—Bryant, Charles. Flora Diaetica: or History of Esculent Plants . . . London, 1783.

p. 212. In section of work entitled "Foreign Berries, often raised in Gardens and Stoves." "*Solanum Lycopersicum* . . . These berries are in such esteem both among the Portuguese and the Spaniards that they are an ingredient in almost all their soups and sauces, and are deemed cooling and nutritive."

1784—Quer, Joseph. Flora Española. Volume V. Madrid, 1784.

p. 386. "It is cultivated in great abundance on the truck farms and irrigated fields in all the provinces and lands of our peninsula; it occurs in great abundance and is sown every year. It flowers by March and April in Andalusia, Murcia and Valencia, so that in these provinces, they enjoy the fruit nearly all year, even in the winter, and I am a witness to having eaten them fresh and recently harvested from the plant in the months of January and February . . .

"The majority of the ancient authors and some modern ones, especially those in the north, still do not agree about the good qualities of the tomatoes. On the contrary, they are of the opinion that they ought to be included in the ranks of the poisonous plants rather than among the medicinal plants. But the experience in our peninsula shows that this is all wrong; and although in Italy, and particularly in Naples, they are eaten with dressing in salads, among us, they are without comparison with other vegetables during their season, for use in sumptuous and delicate dishes, seasoning the most delightful foods and forming a delicious sauce which gives an agreeable flavor to *cocida* and other dishes. The common people use them in cooked dishes and, besides that, eaten in salad and raw with a little salt; they are in general the light breakfast for the field workers in Mancha and Valencia; and a fried dish of tomatoes and peppers forms the afternoon meal and likewise the supper dish of the poor who get fat and strong in the tomato season. Certainly in Spain they are not harmful and are used by the rich and the poor, and neither the former who eat them because they like them nor the latter who eat them out of necessity have suffered the slightest detriménts to their health." (Tr.)

A footnote to the statement, apparently added by someone else, states: "I think that the somewhat excessive eulogy with which the author has paid tribute to the tomato deserves some moderation. Its use, particularly when it is abundant, produces diarrhoeas, fevers, indigestions, and other diseases." (Tr.)

1787—Townsend, Joseph. A Journey through Spain in the Years 1786 and 1787. London, 1792.

Volume I. p. 183. A tomato is listed as one of the plants which the author had obtained dried from the herbarium of a young Barcelonan. He said that he had not seen this plant on any of his walks.

Volume III. p. 271. In a chapter describing Valencia, he describes tomatoes as one of the crops grown in the vicinity of the city. It is described as an "intermediate" crop.

1792—Walters, Johann Jacob. Gartenkunst. Stuttgart, 1792.

p. 118. (See Central Europe, 1792. Walters.)

1794—Barham, Henry. Hortus Americanus. Kingston, Jamaica, 1794.

p. 92. (See West Indies, 1794. Barham.)

1796—Bechstein, Johann M. Naturgeschichte des In- und Auslandes. Leipzig, 1796.

Volume I. p. 333. (See Central Europe, 1796. Bechstein.)

1797—Russel, Alexander. Naturgeschichte von Aleppo. Göttingen, 1797.

Volume I. p. 113. Footnote. (See E. Mediterranean, 1797. Russel.)

1801—Boutelou, Claudio, and Boutelou, Estéban. Tratado de la Huerta. Madrid, 1801.

pp. 375–383. "Tomatoes are cultivated in all the truck farms and gardens of Spain with notable abundance; in foreign countries it is still a little-known plant. However, in the last ten years, the truck farmers in the vicinity of London and Paris have planted some beds on their grounds, and people are beginning to take a fancy to them. Because it is a species of the genus *Solanum* it has been admitted to gardens and fields with reluctance, being suspected of participating in the same qualities, . . . poisonous to men, by which the majority of the species which compose that family in the plant kingdom are distinguished and known.

"Medical and economic uses. They are eaten raw with salt; but it is a cold food and not very healthy. They are also eaten cooked in various ways. Its daily use is for sauces and preserves to which it gives a pleasant acid taste.

"Some prepare them in vinegar with salt and black pepper, making some cuts in them so that the vinegar will penetrate well. Prepared in this way, they last for a long while without spoiling, but not too ripe tomatoes should be used [in this way]. The fruit of the tomato excites the appetite and comforts the stomach suffering from excess heat." (Tr.)

1811—Sickler, J. V. Garten-Handlexikon. Erfurt, 1811.

(See Central Europe, 1811. Sickler.)

1826—Anonymous note. American Farmer. Volume VIII. Baltimore, 1826.

p. 279. (See U. S., 1826. Anonymous.)

1828—Descourtilz, M. E. Flore Pittoresque et Médicale des Antilles, ou Traité des Plantes Usuelles. Volume VI. Paris, 1828.

p. 95. (See France, 1828. Descourtilz.)

1853—Anonymous. "Notizen." Gartenflora. Volume II. Erlangen, 1853.

pp. 248–249. (See Central Europe, 1853. Anonymous.)

EASTERN MEDITERRANEAN

This designation includes the following major political units: Greece, Syria, Iran, Egypt, and Cyprus.

1640—Parkinson, John. Theatrum Botanicum. London, 1640.

pp. 352–354. (See Great Britain, 1640. Parkinson.)

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. (See Great Britain, 1710. Salmon.)

1797—Russel, Alexander. Naturgeschichte von Aleppo. Göttingen, 1797.

Volume I. p. 113. Footnote. "The love apple or tomato which one formerly grew only in pots like other flowers, have quite recently been grown in large quantities and brought into the bazaars; their use was introduced to the French by an Englishman who stayed in Spain and Portugal for some time; the fruit is called by the natives, French Badinjan; it is Linnaeus' *Solanum Lycopersicum.*" (Tr.)

1837—Baumann, Eugene Achille. "Notes taken from the Narrative of a Horticultural Journey in Greece, during the Summer of 1837." The Gardener's Magazine. Volume XV. London, 1839.

p. 102. "Their [Greeks] culinary vegetables consist generally of young pumpkins, not yet fully grown, *Cucurbita Lagenaria?*, with other species and varieties; the fruits and seeds of *Hibiscus esculentus* are used exactly as peas and kidneybeans are here. Their taste is rather sour and very refreshing; tomatoes *(Solanum Lycopersicum)* are used all over the country and in almost every dish."

1839—Anonymous. "How to preserve Tomatoes for the Winter." The Cultivator. Volume VI. Albany, N. Y., 1839–1840.

p. 183. (See U. S., 1839. Anonymous.)

1840—Fiedler, Karl G. Uebersicht der Gewächse Königreichs Griechenland. Dresden, 1840.

p. 757. Says that they grow in practically every garden.

1865—Kotschy, Th. Die Insel Cypern. Wien, 1865.

p. 288. *Lycopersicum.* Common.

1876—Ascherson, P. "Die Garten von Esneh in Aegypten." Gartenflora. Volume XXV. Erlangen, 1876.

p. 71. "In a garden close by the landing place El Homrah at Siut . . . bloomed *Narcissus poeticus* . . . Of vegetables, I found in the *(chedivischen)* garden in Esneh: tomatoes (Arab: *tomat*), egg plant (Arab: *badingan*), etc."

1912—Muschler, Reno. A Manual Flora of Egypt. Berlin, 1912.

Volume II. p. 843. "Cultivated everywhere abundantly; often naturalized."

1952—Interview with Mr. Frank Khinoo.

Mr. Khinoo was a native of Reziah (Urmiah) Province of Iran. His family were Assyrian Christians associated with the produce business in the ancient horticultural center of Gulpashan. He left as a young man in 1918. Mr. Khinoo has had a long association with the growing of vegetables.

He reports that tomatoes are commonly used in northwest Persia, dried into a paste. The process by which the paste is made is as follows: the tomatoes are smashed, skinned, boiled and spread out flat and dried in the sun until gummy. Pieces are cut off of this paste and used for winter cooking. The paste is called "*moorabba bedumdhan.*" Tomatoes are also eaten in a common eggplant dish.

AFRICA
(Exclusive of Egypt)

1671—Addison, Lancelot. An Account of West Barbary. Oxford, 1671. In Pinkerton, John. A General Collection of . . . Voyages and Travels . . . London, 1814.

Volume XV. p. 405. "Besides the salad ordinary in other countries, they have one sort rarely to be met with in Europe which they call by a word sounding Spanish *Tomatés.* This grows in the common fields, and when ripe is plucked and eaten with oil; it is pleasant, but apt to cloy."

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. (See Great Britain, 1710. Salmon.)

1720—Shaw, Thomas. "Travels or Observations relating to Barbary." London, 1757. In Pinkerton, John. A General Collection of . . . Voyages and Travels . . . London, 1814.

Volume XV. p. 601. "Endive, cress, chervil, spinageall, all sorts of beets with the young shoots of the wild and garden artichoke are in season from October to June; and then follow during the rest of the summer calabashes, mellow-keeh, bedinjanms, and tomatas; each of them in its turn gives a relish to their soups and ragouts."

1776—Proyart, ——. Abbé. "History of Loango, Kakongo and other kingdoms in Africa." Paris, 1776. In Pinkerton, John. A General Collection of . . . Voyages and Travels . . . London, 1814.

Volume XVI. p. 554. "The tomato is a small fruit the size of a cherry; the negroes use it as an ingredient in their ragouts as we use onions in ours, but it is from motives of economy and for the sake of filling up, rather than seasoning;

this fruit absolutely insipid of itself, imbibes the taste of the sauce without communicating any of it whatever; it grows on a shrub."

1778—De Cassini, ——. (A Voyage to California by Mons. Chappe D'Auteroche) also A Voyage to Newfoundland and Sallee by Monsieur De Cassini. London, 1778.

p. 186. "These gardens at Sallee likewise abound with water melons, calabashes, meringens, tomatoes and other productions peculiar to hot climates."

1853—Hiern, William Phillip. Catalogue of the Plants collected by Dr. Friedrich Welwitsch in 1853–61. London, 1898.

Volume I. p. 744. *Lycopersicon esculentum.* Barro do Bengo, Loanda, etc. "Wild but not indigenous, very plentifully occurring in all neglected, formerly cultivated places and about dwellings, also at the stations (called *Quilombo*) of the migratory negroes, from the Atlantic shore to Condo, in fields between Quicune and Cacuaco.

"The plant is especially frequent about the fundas (caravan encampments) in company with *Cleome* and *Psidium.*"

1858—Livingstone, David. Missionary Travels and Researches in South Africa. New York, 1858.

p. 712. (From the section of the work, bearing the title "On the Quilimane and Zambesi Rivers, from the Journal of the late Capt. Hyde Parker, R.N., H.M. Brig 'Pantaloon'.").

p. 712. "At one village, about 17 miles up in the eastern bank [of the Zambesi] and distinguished by being surrounded by an immense number of bananas and plantain-trees, a great quantity of excellent peas are cultivated; also cabbages, tomatoes, onions, . . ."

1869—Schweinfurth, Georg. The Heart of Africa. Three Years' Travels and Adventures in the Unexplored Regions of Central Africa from 1868–1871. New York, 1874.

Volume I. p. 121. Along the Gazelle, "I can only boast of having naturalized in this district of Central Africa two plants as representative of the culture of Europe—the sunflower and the tomato."

p. 215. "Here too, I trained some tomatoes and sunflowers which ever since have been quite naturalized in this part of Africa."

p. 253. "The tomato may well be considered a cosmopolite, making itself at home in all warmer latitudes, but previously to my arrival it had not found its way into this region."

p. 528. "I was the first to introduce tomatoes into the district of the Gazelle, and I have no doubt that ere long they will be extensively grown even in the most central localities of Africa."

1872—Oliver, D., and Grant, J. A. "The Botany of the Speke and Grant Expedition." Transactions of the Linnean Society of London. Volume XXIX. London, 1875.

Part I, 1872. p. 119. "The natives at 7° 27′ S. lat. did not know the use of the fruits [of the tomatoes] and were surprised to see us eat them. Frequently met with in the countries between Unyoro and Ugogo."

1873—D'Alviella, Goblet. Sahara and Lapland. Travels in the African Desert and the Polar World. London, 1874.

p. 35. Tomatoes are listed among the crops grown in the gardens in the province of Wady-Suf. These gardens are evidently planted in the bottoms of excavations which are carefully walled to keep them from being filled with blowing sand.

1895—Engler, A. Die Pflanzenwelt Ost Afrikas und der Nachbargebiete. Berlin, 1895.

Part C. p. 356. "Now cultivated everywhere."

Part B. p. 228. "This native American plant is not only cultivated everywhere in the tropics, but has also spread widely in the wild form with little round, hardly cherry-size, brick-red fruits; the wrinkles in the fruits of the larger cultivated forms are not original, but the result of breeding . . .

"They are found everywhere in Africa where civilization has reached; according to Emin, they reached the Equatorial Provinces through the Danagla (Dongolanische Händler); they were still not known to the Dinka- and the Dschurstämmen in Schweinfurth's time (1870); but Junker found them in Bahr el Ghasalgebiet and also among the Mombuttu, cultivated with success by the Mohammedans there.

"In German East Africa, they have penetrated likewise along the path of the Arab traders, and also along the caravan routes. Emin found them in Unyoro in 1877, growing wild in large masses; Stanley mentions them on his Livingstone Expedition as cultivated by the Arabs of Tabora; Baumann mentions them at Kilimani-Urambo; Grant found them at Ugogo; however, the natives of 7° 37′ south latitude still, at that time, didn't know the fruits. One finds them, according to Emin, in Ussui; Stuhlmann found them in Kasinga (westward from Victoria Nyansa) as remnants of the Arab settlement; likewise Kafuro in Karagwe, and also at Kawalli in the ruins of the Arab colony. Naturally, they have been cultivated more recently at missions and military stations. It is noteworthy that the plants have not had a more rapid introduction among the negroes. On the coast it had disseminated itself more freely, for example, in Tangagebiet (Baumann); Bondei (Baumann) and Usambara (Holst); furthermore at Pare (Baumann), even if infrequently, as in Tawetta. It is also found in Usambara everywhere in the plantations and in the vicinity of the houses on the waste places, growing half wild; for this reason, it is seldom planted; it is in that place, of a quite round form, the size of *Mirabellen*, and ripens from May to October; it is brought there in baskets for sale, to be eaten raw or as a side dish with rice or *Ugalli*. Also on the coast, the round *Mirabellen* form is dominant; in Tanga it is used a great deal for a sauce and as a salad, one can obtain ten or twelve tomatoes for one pesa.

"The fruit is not only used raw or cooked for soups, sauces and as a vegetable, but also put in vinegar when unripe to make an excellent, healthy provision.

"They are excellently adapted as vegetables for cultivation at temporary stations; one can provide himself easily with good travel rations with the tomato; after cooking them, one runs them through a sieve or cloth; then boils them down with cayenne pepper; squeezes them out; forms cakes; and allows them to dry for days, with abundant turning, in the sun. (Junker. III. p. 559)." (Tr.)

1905—Gleichen, ——, editor. The Anglo Egyptian Sudan, London, 1905.

Volume I. p. 161. In a discussion of the southwestern Sudan *(Bahr el Ghazal)*, it is reported that the Nyam Nyams grow tomatoes as a food plant.

1906—Johnston, Berry. Liberia. London, 1906.

Volume II. p. 901. "These people [the Spanish and Portugese] who were the great benefactors of East and West Africa as regards the introduction of new food products, also brought to Liberia the pineapple, guava, tomato, capsicum (red pepper), sweet potato, maize, cassava (Manihot), papaw, the orange and lime and the short form of the banana."

p. 990. The tomato is listed among the cultivated plants.

1929—Broun, A. F., and Massey, R. E. Flora of the Sudan. London, 1929.

p. 311. The "*Banaduro*" or "*Tomatum*" is reported as grown throughout the country.

NORTHERN EUROPE

This designation includes the following major political units: Sweden, Latvia, and Norway.

1862—Schübeler, F. C. Die Culturpflanzen Norwegens. Christiana, 1862.

p. 81. "Only admirers, who either find pleasure in the plant itself or who like the taste of the fruit in sauces, bother with their culture." (Tr.)

1867—Andersson, Nils J. Aperçu de la Végétation et des Plantes Cultivées de la Suède. Stockholm, 1867.

p. 75. *Pomme d'amour.* Listed as a cultivated plant under the heading "Condiment Plants."

1952—Interview with Dr. V. Muhlenbach.

Dr. Muhlenbach is a native Latvian and a trained botanist. He reports that the tomato was not eaten in Latvia to any extent before World War I. After the war, it began to be cultivated in large quantities. He thinks it is possible that large numbers of Latvian refugees returning to their homes from Russia brought the habit of using the tomato with them. The tomato was not regarded as poisonous, but rather the taste was thought disagreeable. It is now eaten sliced with onions or preserved as a sauce.

In south Russia at the time of the first World War, Dr. Muhlenbach saw large fields of the plants. They are called tomats in Latvian and pomidor in Russian.

WEST INDIES

1707—Sloane, Hans. A Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica . . . London, 1707.

Volume I. pp. 237–238. "This [the tomato] grows in several places about the Town of St. Jago de la Vega, and in Guanaboa, near Mrs. Guy's House, in her Plantation, but I cannot be positive that 'tis wild. It grows likewise in the Caribes.

"They are eaten by some here, are thought very naughty, and yielding little Nourishment, though they are eaten either boil'd or in a sauce by the Spaniards."

He then proceeds to quote several authors on the tomato.

1750—Hughes, Griffith. The Natural History of Barbados. London, 1750.

p. 148. "They [tomatoes] are generally made use of, boiled in broth. These were brought hither by his excellency Governor Worsley, from Portugal."

1779—Oldendorf, C. G. "Einige Nachrichten zu der Naturgeschichte der Westindischen Inseln." Edited by Jacob Bossart. Sammlungen zur Physik und Naturgeschichte. Volume I. Leipzig, 1779.

p. 234. "The *Solanum lycopersicum* or tomato bears a fruit which, when put on meat and in soup, gives them a flavour." (Tr.)

1798—Manning, Robert, Jr. History of the Massachusetts Horticultural Society, 1829–1878. Boston, 1880.

p. 40. (See U. S., 1798. Manning.)

1828—Descourtilz, M. E. Flora Pittoresque et Médicale des Antilles, ou Traité des Plantes Usuelles. Paris, 1828.

Volume VI. p. 95. (See France, 1828. Descourtilz.)

ASIA

This designation includes the following major political units: India, Burma, Indo China, Malaya, and Dutch East Indies.

1747—Rumphius, Georg Everhard. Herbarium Amboinense. Amsterdam, The Hague, Utrecht. Volume V, 1747.

Volume V. p. 416. Two varieties are described, both apparently used in cookery.

1790—Loureiro, Joannis de. Flora Cochinchinensis. Ulyssipone, 1790.

Volume I. p. 130. Described as growing in the fields and gardens of Cochin China.

1832—Roxburgh, William. Flora Indica. Serampore, 1832.

Volume I. p. 565. *S. Lycopersicum.* "Although this is now very common in India, I suspect it is as little a native as the common potatoe, which is now very generally cultivated over India, even by the natives for their own use."

1837—Blanco, Manuel. Flora de Filipinas. Manila, 1837.

p. 135. "The natives make immense use of the fruit [of the tomato] which they use in almost all their dishes. With their leaves, they dye cotton cloth a dirty green."

The 1845 edition of this work carries the same reference (p. 96).

1865—Birdwood, G. C. M. Catalogue of the Vegetable Productions of the Presidency of Bombay. Bombay, 1865.

p. 173. *Lycopersicon esculentum.* The fruit is reported as eaten as a salad and sauce. It is described as cultivated widely.

1893—Duthie, J. F., and Fuller, J. B. Field and Garden Crops of the North-western Provinces and Oudh. Roorkee, 1893.

Part III. p. 30. Tomato or love apple. "This vegetable is coming more into favour with natives as an article of food on account of its acid taste."

1916—Bamber, C. J. Plants of the Punjab. Lahore, 1916.

p. 403. "This South American plant is widely cultivated . . ."

1932—Ochse, J. J. Vegetables of the Dutch East Indies. Buitenzorg, Java, 1932.

pp. 675–678. Cultivated everywhere in Java. Young and old fruits are eaten as *lalab*, in *sambĕlan (sambĕl gorĕng)* or in *sayoor lodĕh*. The author expressed doubt that the young leaves are eaten as *sepan* with rice as is reported by Hasskarl.

1939—Kanjilal, U. N., *et al.* Flora of Assam. Calcutta, 1939.

Volume III. p. 572. Cultivated throughout the province . . . Flowers and fruits throughout the year.

UNITED STATES

This designation includes the United States and the European colonies which have occupied its continental limits.

1710—Salmon, William. Botanologia. The English Herbal or, History of Plants. London, 1710.

pp. 29–30. (See Great Britain, 1710. Salmon.)

The reference to the presence of the tomato in Carolina in this work antedates by fifty-six years the next mention of the tomato within what was to become a part of the United States. This is apparently an eye-witness report; no hint is given as to the use which was being made of this plant or its fruit.

1766—Bartram, John. "Diary of the Journey through the Carolinas, Georgia and Florida from July 1765 to April 10, 1766." Transactions of the American Philosophical Society. New Series. Volume XXXIII. Part I. 1942.

p. 53 [dated 1766]. "ye 2 nights frost [,] with some ice [,] of ye 4 & 5 of december [,] ye Govenour tould me was harder a Augustine than any they had before crismas last year [.] it killed ye pumpkin vines & many of ye leaves of ye carolina peas but did not hurt ye tomatis [.]"

This mention of the "tomatis" antedates by nearly twenty years the next mention of the plant within what was to become a part of the United States.

From the context it appears that the tomatoes were being used as food plants.

1779—Pieters, A. J. "Seed Selling, Seed Growing, and Seed Testing." Yearbook of the United States Department of Agriculture, 1899. Washington, 1900.

p. 568. "In New Orleans they were used in catsup as early as 1779, but in the English colonies tomatoes were planted only as ornament, under the name of 'Love apples'."

This reference is not documented.

1782—Jefferson, Thomas. Notes on the State of Virginia. Baltimore, 1800.

p. 41. "The gardens yield musk-melons, water-melons, tomatoes, okra . . ."

The same quotation is reported to appear in the 1782 edition of the work. (Jefferson's *Garden Book*. p. 648—see 1809 below. Jefferson.)

1784—Boyd, James. A History of the Pennsylvania Horticultural Society, 1827–1927. Philadelphia, 1929.

pp. 22–23. "For several years the Landreths [David Landreth Seed Co.] were the only florists to introduce vegetables, fruits and flowers to the citizens of Philadelphia. They labored under difficulties as they had to make all their sales from a garden stall, by the side of the old Court House. Later, other gardeners, florists, and seeds men took up this work as the desire for rare products increased. Tomatoes, ochra, and artichokes were first demanded by the French immigrants and there was little sale for them to others. Afterwards, cauliflower, head lettuce, egg plant, oyster plant, cantaloupes, rhubarb and sweet corn were introduced."

This reference comes from a section of the work dated 1784.

1785—Varlo, C. A New System of Husbandry. Philadelphia, 1785.

Volume II. p. 291. In an article entitled "The Gardeners Calendar, for Work to be done round the Year in the Kitchen Garden," tomatoes are listed under "March."

1792—Imaly, G. A Topographical Description of the Western Territory of North America. London, 1792.

p. 88. Tomatoes are not listed in a rather long list of culinary plants and vegetables grown in the upper settlements on the Ohio.

1794—M'Mahon, Bernard. A Catalogue of Garden, Grass, Herb, Flower, Tree & Shrub-Seeds, Flower-Roots &c, &c. Sold by Bernard M'Mahon, Seedsman.

A single broadside sheet. Under Seeds of Annual Flowers, are listed: Tomatoes, or Love Apple. Mr. Edward C. Vick of Newark, New Jersey, who discovered this early catalogue, first dated it at 1804. A thirty-page catalogue of M'Mahon's issued in 1804 was subsequently discovered and this broadside sheet was then dated at eight to ten years earlier, 1796–1794.

1798 and **1802**—Manning, Robert, Jr. History of the Massachusetts Horticultural Society, 1829–1878. Boston, 1880.

p. 40. "The tomato was introduced into Salem about 1802, by Michele Felice Corne, an Italian painter; but he found it difficult to persuade people even to taste the fruit. It is said to have been introduced into Philadelphia by a French refugee from St. Domingo, in 1798. It was used as an article of food in New Orleans in 1812, but was not sold in the markets of Philadelphia until 1829. It did not come into general use in the North until some years later after the last-named date."

p. 248. A premium is offered in 1839 by the Massachusetts Horticultural Society for the first time for the best tomatoes.

p. 344. "As perhaps the most striking instance of improvement we may mention the tomato, now universally used, but in 1845 comparatively unknown."

1802—Anonymous note. The Cultivator. New Series. Volume IX. Albany, N. Y., 1852.

p. 381. "It is said that this fruit, which is of very modern introduction into our gardens, has been in long use by the French and Italians—and that among the old French settlers, on the banks of the Kaskaskia, in Illinois, it has been cultivated for more than fifty years."

1803—Gleanings from the Most Celebrated Books on Husbandry, Gardening and Rural Affairs. Philadelphia, 1803.

p. 194. Love-apple *(S. Lycopersicum)*. The culture of this plant is described. Two varieties, one red and the other yellow, are listed. Under uses: "The fruit in medicine; also for sauces, soups, and pickling."

This edition is identical to a London edition, also of 1803.

1804—Gardiner, John, and Hepburn, David. The American Gardener. Washington, 1804.

p. 27. "Sow love apples . . . The fruit is used for soups and pickles."

1804—Willdenow, C. L. Anleitung zum Selbststudium der Botanik. Berlin, 1804.

p. 167. (See Central Europe, 1804. Willdenow.)

1806—M'Mahon, Bernard. The American Gardener's Calendar. Philadelphia, 1806.

p. 200. "The different varieties of the Capsicums, Tomatoes, and Eggplants . . . are in much estimation for culinary purposes . . ."

p. 319. "The *Solanum Lycopersicum*, Tomato, or Love-apple is much cultivated for its fruit, in soups and sauces to which it imparts an agreeable acid flavour; and is also stewed and dressed in various ways, and very much admired."

1809—Hosack, David. A Catalogue of Plants contained in the Botanic Garden at Elgin, New York, 1809.

p. 26. *Solanum lycopersicum* is listed.

1809—Squibb, Robert. Gardeners Calendar for North Carolina, South Carolina and Georgia. Charleston, 1809.

p. 52. Sow tomatoes.

p. 76. Transplant.

p. 90. Stake, etc.

The same reference appears in the 1827 edition of this work with different pagination (pp. 59, 83, 98).

1809–1814—Jefferson, Thomas. Thomas Jefferson's Garden Book. 1766–1824. Annotated by Edwin M. Betts. Philadelphia, 1944.

p. 391. Tomatas from G. Divers are noted in the Garden Kalendar for 1809.

p. 403. In a letter from General John Mason to Jefferson from Analoston on Jan. 22, 1809: "J. Mason presents his respects and with very great pleasure sends him the garden seeds asked in his note of the other day, in addition to which he begs his acceptance of the few of the *Buda Kale*—and excellent variety of cantaloup—Spanish tomata."

p. 470. Tomatas are listed as "come to the table" on August 14, 1812.

p. 506. Although his seed stocks are scanty he sends Randolph several varieties, including tomatas.

p. 536. Reports that tomatas were killed by frost on May 9, 1815.

p. 613. A letter from Mexico dated March 21, 1824, encloses tomatas to care of W. [Mc] Andrews for Mr. Jefferson.

p. 639. In "A Statement of the Vegetable Market during a period of 8 years wherein the earliest and latest appearance of each article within the whole 8 years is noted," the dates listed for tomatoes are July 16 and November 17.

Reference is made to the tomato in several lists and gardening calendars in addition to those mentioned above. The index to this work contains a full listing of these. (See 1845, Anonymous. "The Tomato," below.)

1811—Hosack, David. Hortus Elginensis, or a Catalogue of Plants indigenous and exotic, cultivated in the Elgin Botanic Garden. Second edition. New York, 1811.

p. 53. Lists *Solanum Lycopersicum* as a culinary vegetable. (See 1809 above. Hosack.)

1812—(See 1798 above. Manning.)

1819—The Practical American Gardener, by an old Gardener. Baltimore, 1819.

pp. 57, 71, 87, 94, and 101. Tomatoes are listed with directions for their handling at various times of the year. The plant is listed in the table of contents of this work under the heading, "Kitchen Garden Esculent Plants, &c."

1819—M'Murtrie, R. Sketches of Louisville. Louisville, 1819.

p. 226. In *Florula Louivillensis*. *Solanum lycopersicon* is listed as a cultivated plant.

1820—Anonymous note: From the Practical American Gardener for the Month of May. American Farmer. Volume I. Baltimore, 1820.

p. 36. Directions are given for sowing tomatoes. (See 1819 above. The Practical American Gardener.)

1820—Helfer, Harold. "Love Apple." The Farm Quarterly. Volume VII. Number 1. Spring, 1952.

p. 48. "One of the unsung heroes of our country was Robert Gibbon Johnson, a great man who made a lasting and profound contribution to our society, and was then forgotten. Hardly any one ever heard of this man, much less of his brave act on the courthouse steps at Salem, N. J., on a hot August day in 1820 . . .

". . . his claim to fame rests on neither his wealth nor the honors that were thrust upon him.

"Robert Gibbon Johnson deserves immortality because he ate a tomato."

The article implies that through Johnson's public consumption of the tomato its popularity was greatly enhanced.

Helfer also reports that the name "Love Apple" is applied because a "red, ripe tomato was sometimes presented by a shy swain to his sweetheart as a token of his love."

1820–1875—Interview with Mrs. Minnie Du Bose Horner (neé Winans).

Mrs. Horner is an alert, intelligent, and charming southern lady of 93. She was born on a plantation near Shreveport, Louisiana, on May 29, 1859. Her memory, however, includes events, by virtue of stories told her by her grandfather, back to at least 1820. As she recalls, her grandfather told her that when he was a boy (about 1820) in Virginia, people thought tomatoes were poisonous, and used the ripe fruit as mantle decorations. She herself remembers an older sister eating tomatoes right off the vine with a little salt. On one occasion, the sister ate so many in this fashion that she made herself ill. This event is approximately dated 1864.

In the period around 1869, Mrs. Horner was sent to a girls school at Mansfield, Louisiana. She recalls how she experienced a sudden craving for tomatoes during a minor illness in the early winter. A stray tomato was found on the frost-bitten vines and brought in for her to eat.

The family moved to Columbia, Missouri, in 1873. There Mrs. Horner remembers a keen competition between her grandfather and a neighbor to see who could raise the earliest tomatoes. At this time the fresh fruit was commonly used. Before satisfactory canning techniques were developed, the tomato was frequently made into a sweet preserve or pickle.

1822—Anonymous note. American Farmer. Volume IV. Baltimore, 1822.

p. 40. A farm wife describes her trouble with bed bugs, and how she got rid of them. It seems that while she was walking in the garden she accidentally touched a tomato vine which was particularly nauseous in smell to her. It occurred to her that the smell might also be nauseous to the bed bugs. She rubbed the bedstead with a tomato vine, and presto! No bed bugs.

1822—Anonymous recipe. American Farmer. Volume IV. Baltimore, 1822.

p. 208. A recipe is given for the preservation of tomatoes for the winter. It involves cooking them with salt, pepper, ginger, and garlic and then bottling them.

1823—Anonymous recipe. American Farmer. Volume V. Baltimore, 1823.

p. 215. A recipe for tomato catsup is printed.

1825—Sturtevant, E. Lewis. "Kitchen Garden Esculents of American Origin III." American Naturalist, 1885.

p. 668. Without documentation, Sturtevant says that the tomato was grown in western New York for the first time in 1825 from Virginia seed. He also reports that "Mr. T. S. Gold, secretary of the Connecticut Board of Agriculture, writes me that 'we raised our own tomatoes about 1832, only as a curiosity, made no use of them though we had heard that the French ate them. They were called love apples'."

This article contains several other partially documentated references to the early use of the tomato in the United States. These incomplete references are included in the body of this bibliography. (See also 1919 below. Sturtevant.)

1826—Anonymous note. American Farmer. Volume VIII. Baltimore, 1826.

p. 279. Love Apples. "An ingenious mode has lately been discovered in Spain, of preserving for an indefinite time, the perfume and other qualities of the tomato, and of conveying it to great distances in a small compass. This process consists in pulverizing the fruit after having dried it in the sun and in an oven. To preserve the powder, all that is necessary is not to expose it to the air."

1826—Anonymous note. American Farmer. Volume VIII. Baltimore, 1826.

p. 261. "A gentleman in New London, near Lynchburg, has raised a tomato 2 feet and 3 inches in circumference."

1826—Darlington, William. Flora Cestrica. West-Chester, Pennsylvania, 1826.

p. 117. S. *Lycopersicum*. "We have a variety with the fruit smaller, and not torulose. This plant is cultivated for the sake of the mature fruit which is of a sprightly acid taste,—and much admired by many as a sauce, with meats."

1827—Cousin Tabitha. "Recipe for Tomato Ketchup." American Farmer. Baltimore, 1827.

p. 191. ". . . To my taste this is superior to any West India ketchup that I have ever met with, and is withal an excellent remedy for dyspepsia."

1828—Anonymous recipes. The Southern Agriculturist. Volume I. Charleston, 1828.

p. 143. Two recipes are given: (a) Tomato sauce for cold meat, and (b) Potted Tomatoes.

1828–1838—White, William N. Gardening for the South. New York, 1868.

p. 312. Quotes Robert Buist as writing, "that as an esculent plant in 1828–29, the tomato was almost detested, yet in ten years more every variety of pill and panacea was 'extract of tomato'."

1829—Anonymous. "On raising tomatoes from cuttings" (originally from the Southern Agriculturist). American Farmer. Volume XI. Baltimore, 1829.

pp. 164–65. The article describes the method of raising tomatoes from cuttings and describes a technique for ripening which yields tomatoes for Christmas.

1829—(See 1789 above. Manning.)

1830—Blake, Eli W. "Acid in Tomatos." The American Journal of Science and Arts. Volume XVII. New Haven, 1830.

p. 115. "I would suggest to your sir . . . the idea of examining the acid contained in Tomatos. I have observed that it acts powerfully on tin, which I believe is not common with the vegetable acids. I have observed this fruit has the remarkable property of imparting a beautiful orange color to animal oils."

1831—Anonymous. "On Plantation Gardens and the Culture of Vegetables." The Southern Agriculturist. Volume IV. Charleston, 1831.

p. 81. "So general a favorite is the tomato and so eagerly sought after and desired on our table, that we may be excused for diverging a little from our subject, whilst we give a process by which they can be had throughout the winter." He then proceeds to describe a technique by which the tomato is dried in slabs and pieces broken off as needed throughout the winter.

1831—Anonymous. "Letter to Mr. Fessenden." The Southern Agriculturist. Volume IV. Charleston, 1831.

p. 503. "As tomatoes have, at last, become common in our market, I send you a recipe for preserving them during winter. Besides the numerous modes of preparing this delicious vegetable for the table, it may be stewed, etc." A recipe for the preservation of tomatoes follows.

1832—Anonymous note. American Farmer. Volume XIV. Baltimore, 1832.

p. 222. The article quotes Gerarde on tomatoes as a food, (. . . they yield very little nourishment to the body and the same naught and corrupt.—see Great Britain, 1597. Gerarde), and continues: "His [Gerarde's] opinion of the tomato as an article of food might find advocates in the present day, among those who have only tasted, but who have not given them a fair trial. To most persons the flavor is disagreeable at first which a little use entirely counteracts or removes. The culture of this fine fruit ought to be more extensively introduced amongst our countrymen."

1832—Anonymous recipe. (Originally from the Southern Planter and Family Lyceum.) American Farmer. Volume XIV. Baltimore, 1832.

p. 286. A recipe for Tomato preserves "which tastes so much like peach preserves it can serve as a substitute."

1832—Anonymous letter. (Originally from the Southern Agriculturist.) American Farmer. Volume XIV. Baltimore, 1832.

p. 350. The writer sends in some seeds of the "Mississippi tomato" noting that "they are found bordering on the Mississippi swamp, spreading an unusual length, forming a beautiful vine, ornamental; and the seed growing in clusters resembling grapes."

The letter is dated Buffalo, Sept. 10, 1832.

1832—(See 1825, Sturtevant, above.)

1833—Bridgeman, T. The Young Gardener's Assistant. N. Y., 1833.

p. 69. Tomato. "The tomato or Love Apple is much cultivated for its fruit in soups and sauces to which it imparts an agreeable acid flavour; and is also stewed and dressed in various ways, and very much admired."

1833—Anonymous note. American Farmer. Volume XV. Baltimore, 1833.

p. 121. It is reported in the June 28, 1833 issue, that "ripe tomatoes were sold in Market on Wednesday, 19th instant, by Mr. Frieze's gardener" for fifty cents a dozen.

1833—Anonymous note (originally from the Genesee Farmer). American Farmer. Volume XV. Baltimore, 1833.

p. 407. A method for the raising of early tomatoes is described. The author adds, "In this way I never fail to have abundance of this wholesome and delicious vegetable."

1834–1854—Brown, D. J. "The Tomato." Report of the U. S. Commissioner of Patents for the Year 1854—Agriculture. Washington, 1854.

p. 385. "The tomato, until within the last twenty years, was almost wholly unknown in this country as an esculent vegetable, and only to be found in borders and flower gardens, for ornament and curiosity, under the name of 'Love apple.' Since its introduction to the uses of the table, and the discovery of its exceedingly wholesome properties, it has been rapidly gaining favor, and is now one of the most common of all culinary vegetables. It is extensively grown near the large markets, where its high price early in the season is a great inducement to gardeners to undertake to produce an early crop."

Following this quoted material there is a description of the method of cultivation and of winter ripening, and a list of varieties with their particular uses. Some are noted as being especially good for pickling or for preserves.

1834—(See 1798 above. Manning.)

1835—Anonymous. "The Tomato." The Cultivator. Volume II. Albany, N. Y., 1838 (a republication of the 1835 edition).

p. 94. "Dr. Bennet, a medical professor in one of the western colleges, considers the tomato as an invaluable article of diet. He ascribes to it high medicinal properties and declares, '1st. That it is one of the most powerful deobstruents (i.e. removing obstructions; having the power to clear or open the natural ducts of the fluids and secretions of the body; resolving vicidities; aperient) of the materia medica.

" '2nd. That a chemical extract will probably soon be obtained from it which will altogether supersede the use of calomel in the cure of diseases.

" '3rd. That he had successfully treated serious diarrhoea, with the article alone.

" '4th. That when used as an article of diet it is almost a sovereign for dyspepsia, or indigestion.

" '5th. That persons moving from east or north, to the west or south, should by all means make use of it as an aliment as it would in that event save them from the danger attendant upon those violent bilious attacts which almost all unacclimated persons are liable to.

" '6th. That the citizens in general should make use of it, whether raw or cooked or in the form of a catsup, with their daily food as it is the most healthy article of the Materia Alimentary, &c., &c!'

"Without intending to indorse all of the professor's conclusions, we know enough of this vegetable from experience to recommend it as a grateful vegetable, and salutary to health in the summer months.

"It is extensively used in the south and southwest as an article of diet. It is easily cultivated, and readily prepared for the table in various forms, requiring merely a seasoning of salt and pepper . . ."

1835—Maine Farmer. August 21, 1835.

It is reported that in one of the western colleges about this time, a Dr. Bennet refers to the tomato or "Jerusalem apple" as being found in abundance in the markets. (See 1825 above. Sturtevant.)

1835—Maine Farmer. September 11, 1835.

In the *New York Farmer* of this period, one person is mentioned as having

planted a large number of plants for the purpose of maturing fruit for the making of sauce. (See 1825 above. Sturtevant.)

1835—Maine Farmer. October 16, 1835.

An editorial on the tomato says that it is cultivated in gardens in Maine and is "a useful article of diet and should be found on everyman's table." (See 1825. Sturtevant, above.)

1835—Corbett, L. C.; Gould, H. P.; *et al.* "Fruit and Vegetable Productions." United States Department of Agriculture Yearbook, 1925. Washington, 1926.

p. 415. "There are abundant evidences that the tomato or 'love apple,' as it is called, was considered poisonous by the majority of the American people prior to 1835. Elizabeth Clark, who was born in Trenton, N. J., in 1833, related during her lifetime how when as a child she gathered and ate the 'love apple,' but when caught in the act she was rushed to the doctor with the fear that she had been poisoned and would probably not survive."

1837—Darlington, William. Flora Cestrica. West-Chester, Pennsylvania, 1837.

p. 137. S. *Lycopersicum.* "This is cultivated for its fruit,—which is much esteemed by many persons as a sauce or condiment, and is, of late years, coming into very general use."

1837—Anonymous. "The Tomato." The Cultivator. Volume IV. Albany, N. Y., 1837–38.

p. 62. "We are receiving new evidence of the utility of this grateful garden vegetable in preserving health, and in curing indigestion and diseases of the liver and lungs. A writer in the *Farmer's Register* says it has been tried by several persons to his knowledge with decided success. They were afflicted, says he, with a chronic cough, the primary cause of which in one case was supposed to be a diseased liver—in another a diseased lung. It mitigates, and sometimes effectually checks a fit of coughing. It was used in a dried state, with a little sugar mixed with it, to render it more agreeable to the taste. The writer expresses a conviction that, if freely used in July, August, and September, it would prove a complete antidote to bilious fever. [Then follows a method for cultivating the tomato and drying it in the sun.] We consider the tomato and rhubarb the most healthy products of the garden.

"Professor Rafinesque says of the vegetable, 'It is everywhere deemed a very healthy vegetable, and an invaluable article for food.'

"Professor Dickson writes, 'I think it more wholesome than any other acid sauce.'

"Professor Dungilson says—'It may be looked upon as one of the most wholesome and valuable esculents that belong to the vegetable kingdom'."

1838—Anonymous note. The Cultivator. Volume V. Albany, N. Y., 1838–39.

p. 184. "There has been, of late, so much said in commendation of this vegetable as promotive of health, that *we* need not recommend its culture. It is a grateful and healthy vegetable in many ways to those who are accustomed to its use . . . They are an excellent ingredient in soups, make a good catsup, stewed in their own liquor they are a fine sauce for meats; they may be dried or pickled; and they are made the basis of a medicine which, if we are to credit the declarations of the venders, is an infallible cure for most all sorts of diseases which man is heir to."

1838—Lelievre, J. F. Nouveau Jardinier de la Louisiane. Nouvelle-Orleans, 1838.

p. 109. *Tomate (Pomme d'Amour).* "Many species are known all of which are used in cooking and are equally good.

"One can use them to decorate a partition, a wall or the lower part of a garden house, where they produce a nice enough effect through the tender green of their leaves and the rose of the fruit standing out [against them]."

1839—Farnham, Thomas J. "Travels in the Great Western Prairies, the Anahuac and Rocky Mountains and in the Oregon Territory." Travels in the Far Northwest. Edited by Reuben Gold Thwaites. Cleveland, Ohio, 1906.

Volume I. p. 334. Tomatoes are reported among the crops being grown in September, 1839, at the Whitman Mission near Walla Walla.

p. 337. "The breakfast being over, the doctor invited me to a stroll over his premises. The garden was first examined; its location on the curving bank of the Wallawalla; the apple trees, growing thriftily on its western border; the beautiful tomatos and other vegetables burdening the grounds."

1839—Anonymous. "How to Pickle Tomatoes." The Cultivator. Volume VI. Albany, N. Y., 1839–40.

p. 134. "Daily use of the tomato: cut up with salt, vinegar and pepper (as you do cucumbers) and eat away as fast as you can."

Recipes for pickling and stewing tomatoes are also printed.

1839—Anonymous. "How to preserve Tomatoes for the Winter." The Cultivator. Volume VI. Albany, N. Y., 1839–40.

p. 183. "Among other improvements in horticulture, I have been gratified to observe the increased cultivation of the tomato. Believing this to be a most healthy vegetable, I send you an account of the manner in which universally in Asia Minor, they are preserved for use during the winter . . . [Then follows a method for preserving fruit involving treatment with salt, running through a collander, and sun drying in shallow dishes. The dried material of jelly-like consistence is stored in jars.]

"A tablespoonful of this tomato jelly is enough to impart a relish to a dish of pilaf, that is, rice cooked with meat or butter, or soup, for a large family."

1839—(See 1798 above. Manning.)

1840—Dewey, Chester. Report on the Herbaceous Flowering Plants of Massachusetts. Cambridge, 1840.

p. 166. *Solanum lycopersicum* L. Tomato. "The specific name is from the Greek for *wolf* and *peach*, from the beauty of the fruit and its deceitful value.—Loudon. The estimate of the fruit seems to be much changed. It has for some time been 'one of the most important articles used in Italian cookery,' and in England and this country its cultivation has greatly increased, and it is now a very agreeable and important vegetable. Its peculiar acid seems to be most grateful to the stomach, and in many instances has averted the evils of dyspepsia and kindred affections. A professed extract of the fruit has been prepared for use, when the fruit cannot be obtained. The danger of imposition upon the public in all such cases need only be adverted to. The fruit, plucked before it is ripe, is often pickled. The preservation of the fruit in some way, by which its properties should not be essentially altered, is a great desideratum for dyspeptics . . ."

1841—Russell, J. W. "On the Culture of the Tomato and Egg Plant." Magazine of Horticulture. Volume VII. Boston, New York, 1841.

p. 97. "The Tomato *(Solanum lycopersicum)* is of the same family of plants as the potato *(Solanum tuberosum)*; the French and Italians, particularly the latter, think as much of a field of tomatoes as a New England farmer does of a choice field of potatoes.

"Tomatoes are so well known, that the fruit, when ripe, has become almost an indispensable dish through the summer months, on every table. The modes of cooking it are various according to the taste and fancy of individuals, and it would, I conceive, be altogether unnecessary to describe them."

1841—Anonymous note. The Cultivator. Volume VIII. Albany, N. Y., 1841.

p. 76. "The tomato has within a few years acquired much celebrity as a garden vegetable, and to most palates, it is as delicious as it is certainly conducive to health . . . Those who have not hitherto cultivated this plant will do well to introduce it into their gardens."

1842—Hooker, Edward James. The Practical Farmer, Gardener and Housewife. Cincinnati, Ohio, 1842.

p. 493. The author says that the tomato has recently been found a sovereign remedy for dyspepsia and for persons with too much bile. He notes that the discovery was made "last summer" and has greatly increased consumption.

According to this report, you can't lose with this vegetable. What can't be sold raw can be sold as catsup. Hooker reports that "one gentleman last year cleared $1,000 by rearing this article on a small farm near the city."

The author predicts that in 1843 there will be four times as many users of the fruit as there were in 1842. Recipes for Tomato Sauce, Omelet, etc. are listed.

He concludes, "The tomato has become a great favorite, sliced and seasoned as we do the cucumber, and has the advantage of being quite wholesome."

1842—Anonymous. "The Kitchen Garden." The American Agriculturist. Volume I. New York, 1842.

p. 91. "There are but few who relish the tomato at the first taste; and few who are not extremely fond of it when properly cooked and they become accustomed to it. It is considered by physicians and others acquainted with its effects, not only a very delicious, but a very wholesome vegetable; indeed, some will give a decided preference of a dish of tomato sauce or a tomato pie when properly prepared to anything of the kind in the vegetable kingdom.

"There is no vegetable more easily raised and none better pay the cultivator where they arè generally known. They are used in various ways, either raw, with sugar, or stewed for sauce or in fricasses and soups for catsup or gravy, for meat and for pies, or preserves, as well as for pickles and sweet meats."

1842—Anonymous. "The Tomato." The Cultivator. Volume IX. Albany, N. Y., 1842.

p. 165. "The Wayne *Sentinel*, published at Palmyra in this state, informs us that ripe tomatoes grown upon a last year's plant, which as an experiment had been preserved through the winter in a box and set out in the garden in May, were picked by one of our citizens early in August. This is a simple and cheap, if not new mode, of obtaining an early supply of this valuable and delicious vegetable and will no doubt be enlarged upon hereafter'."

1842—Anonymous. "The Tomato and its Uses." The Cultivator. Volume IX. Albany, N. Y., 1842.

p. 167. "Every body cultivates the tomato and every one who has not deliberately made up his mind to be ranked among the nobodies has learned to eat it. There is a great deal of fashion in this, it must be confessed, but it is not often that fashion is active in forwarding so good a work; for if the opinions of numerous M.D.'s of great celebrity, are to be allowed of any weight there are a few things more conducive to health than a liberal use of tomatoes. The fruit has long been extensively used in Italy and the South of France, and within a few years, its cultivation as an article of luxury, if not of necessity, has spread over the greater part of Europe and the United States. The fruit is the best in a warm climate where it has an acidity and briskness unknown in a colder one. In our southern states, the fruit is finer and the flavour richer than in the northern ones; still, in these last, abundance of tomatoes of excellent quality are grown . . .

"Frequent inquiries are made by those who have but lately commenced their cultivation as to the best modes of cooking or preserving them . . ." [Then follows a long list of recipes including: tomato catsup; sliced tomatoes with salt, vinegar and pepper or with sugar; tomato soy; tomato omelet; tomato as a relish for beefsteak; stewed tomatoes; tomato preserves; tomato pickles; tomato figs; tomatoes for winter.]

1843—Burr, Fearing, Jr. Field and Garden Vegetables of America. Boston, 1862.

p. 639. "In this country its [the tomato's] cultivation and use may be said to have increased fourfold within the last twenty years; and it is now so universally relished, that it is furnished to the table in one form or the other, through every season of the year. To a majority of tastes, its flavor is not at first particularly agreeable but, by those accustomed to its use, it is esteemed one of the best as it is reputed to be one of the most healthful of all garden vegetables."

1844—Anonymous. "Garden Vegetables." The Cultivator. New Series. Volume I. Albany, N. Y., 1844.

p. 100. "The Tomato, though now much more common than formerly, is still not to be found in many farmer's gardens, where it should be certainly, if the mandates of imperious fashion are in any degree to be heeded. The tomato, though found in its greatest perfection in southern latitudes, can with a little attention be grown in most of our gardens and furnish for months a wholesome and, to many, a most agreeable article of food. Few like the tomato at first, but . . . soon become not only reconciled to it, but are much pleased with it . . .

"There are several varieties of the tomato, but the large red for the table or preserving, and the cherry tomato for pickling are perhaps the best. They are used in various ways, eaten in vinegar as cucumbers, made into soups, into toasts, baked in pies, but perhaps the greatest use is in tomato sauce which is highly esteemed.

"There can be no doubt that our farmers might, at a little expense, greatly enlarge their list of garden esculents; and in doing so materially decrease their annual expenses, while they are at the same time adding to their comforts."

1845—(See 1798 above. Manning.)

1845—Beecher, ——. "Cooking Tomatoes." The Cultivator. New Series. Volume II. Albany, N. Y., 1845.

p. 321. "Mr. Beecher of the Indiana *Farmer* speaks with the enthusiasm of an epicure on the subject of tomatoes. He says that whoever does not love them, 'is an object of pity.' There's no accounting for taste. The editor of the Boston *Courier*, for instance, repudiates Mr. Beecher's taste and compares tomatoes to 'rotten potatoe-balls'."

1845—Anonymous. "The Tomato." The American Agriculturist. Volume V. New York, 1846.

p. 282. "Thomas Jefferson Randolph, the protegé of Jefferson, in an address before the Agricultural Society of Albemarle County, Virginia, delivered some time ago, stated that Mr. Jefferson could recollect when the tomato was cultivated as an ornament to the flower-garden and deemed poisonous." (See 1809 above. Jefferson.)

1845—Anonymous note. The American Agriculturist. Volume V. New York, 1846.

p. 303. "Mr. Meigs read from the 'Annals of the Royal Horticultural Society of Paris' an account of a successful experiment in grafting a stem of the tomato

upon the stalk of a potato, by which a crop of tomatoes was raised in the air and one of potatoes in the earth."

1847—Johnson, George W. A Dictionary of Modern Gardening. Edited by David Landreth. Philadelphia, 1847.

p. 590. "This plant is a native of South America, and perhaps of the West Indies; thence introduced into this country. But a few years since, it was scarcely known as an esculent—now it is in very general use."

1848—Munson, W. M. "Tomato Notes." West Virginia Agricultural Experiment Station, Morgantown, W. Va. Bulletin 117. June 1, 1908.

p. 251. "The credit of introducing canned tomatoes as an article of trade is due to Mr. Harrison W. Crosby, who made his first venture in 1848, while steward of Lafayette College, Easton, Pennsylvania. There was a ready demand for the goods, and with increased supply and improved machinery, the cost has been reduced from 50 cents per can in 1848 to 7 cents at the present time."

1850—Goodrich, C. "Raising Tomatoes in Vermont." Magazine of Horticulture. Volume XVI. Boston, 1850.

p. 330. "I noticed in the *Horticulturist* for June, among the 'Answers to correspondents' one to a 'Vermont subscriber' in which the editor says, 'Your season is not quite long enough for the okra or tomato.' If he will visit us in this '*Northern* part of Vermont,' in August, September, October, or November, we will engage to give him a full supply of tomatoes; and will CONTRACT to freight one of our *lake craft* with them and send him at the price of potatoes. No vegetable is here more easily grown or so freely given away. They are raised with no trouble but thinning and cultivating the plants, which grow abundantly from self sown seeds . . . Yours, C. Goodrich, Burlington, Vermont. May, 1850."

1851—Neill, Patrick. The Fruit, Flower and Kitchen Garden. Adapted to the U. S. from the 4th Edition. Philadelphia, 1851.

p. 236. Reports that the tomato is of immense consumption in the South and Middle states, and is the object of intensive field cultivation in the neighborhood of Philadelphia.

1853—Anonymous. "Notizen." Gartenflora. Volume II. Erlangen, 1853.

pp. 248–249. (See Central Europe, 1853. Anonymous.)

1862—Boswell, Victor R. "Improvement and Genetics of Tomatoes, Peppers, and Eggplant." United States Department of Agriculture Yearbook, 1937. Washington, 1937.

p. 179. A tomato variety by the name of "Fiji Island" was introduced into the United States in 1862. (See South Pacific, 1838. Wilkes.)

1919—Sturtevant, E. Lewis. Sturtevant's Notes on Edible Plants. Edited by U. P. Hedrick. Report of the New York Agricultural Experiment Station for the Year 1919. II. Albany, 1919.

pp. 343–348. Sturtevant presents a detailed study on the history of the

tomato, etc. Most, if not all, of the references quoted by Sturtevant in the above work, are included, if pertinent, in this bibliography.

Earlier and only slightly different versions of this same article appeared in 1885, Sturtevant, above, and in the *Report of the Maryland Agricultural Experiment Station*, 1889 (pp. 18–25).

SOUTH PACIFIC

1838–1842—Wilkes, C. Narrative of the U. S. Exploring Expedition. Philadelphia, 1845.

Volume III. p. 309. "The Feejee tomato *(Solanum)* in its green state was first seen at Tavea. . . . The tomato, already spoken of, was found here in its ripe state. It is believed to be a perennial plant. The fruit is the size of an orange, and of an agreeable flavour; it has been grown and ripened in Philadelphia, and I am in hope will in a short time be acclimated in the United States, where it will be a great acquisition."

p. 335. "The new species of tomato *(Solanum)* of which mention has already been made, may be almost classed with the fruits; it is cultivated by the natives on account of its fruit, which is round, smooth, and about the size of a large peach; when ripe, its colour is yellow; its taste was by some thought to have a strawberry flavour. We have made every endeavor to introduce the plant into the United States by sending home seeds, some few of which have fallen into good hands, and been taken care of; but I regretted to find the greatest part had been distributed to those who had not taken any care in its cultivation. Fruit from the seeds had, however, been produced in Philadelphia. The plant will, no doubt, succeed in the southern section of the Union. It is supposed to be biennial. There were two smaller varieties of the same species, which the nativès eat, and which are about the size of an egg." (See U. S., 1862. Boswell.)

1839—Anonymous. "Foreign Notices." Gardener's Magazine. Volume XV. London, 1839.

p. 475. Tomatoes are listed among the vegetables for which prizes were awarded at a show of the Sydney Floral and Horticultural Society. The account is reprinted from the Sydney *Monitor* of February 15, 1839.

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New scientific names of plants and the final members of new combinations are printed in **bold face** type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.

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